

Spatial distribution modelling reveals climatically suitable areas for bumblebees in undersampled parts of the Iberian Peninsula

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1 Spatial distribution modelling reveals climatically suitable areas for bumblebees in
2 undersampled parts of the Iberian Peninsula.

3 Find the bee before it is too late: Iberian Peninsula has large undersampled regions in
4 climatically suitable areas for bumblebees

5 Authors: Andreia, Hugo, Dave

6 ABSTRACT

7 The Iberian Peninsula supports a high diversity of bumblebees, with 38 species all of which are
8 at or near the south western edge of their range. We might expect them to be threatened by
9 climate change, but their distributions within Iberia are poorly documented. In this study we
10 examine the climatic conditions that explain the distribution of Iberian bumblebees. Spatial
11 distribution models (SDMs) were built using a presence-only technique (Maxent),
12 incorporating presence data of Iberian bumblebees (initially 5,795 records for 38 species) with
13 seven climatic variables. We observed that: 1) mountain regions were highlighted as rich in
14 species (bumblebee hot-spots); 2) rare species are climatic specialist species that mainly inhabit
15 mountain regions; 3) common species are more tolerant of a broader range of climates, notably
16 of higher temperatures; 4) some areas of Iberia are largely undersampled, including areas
17 predicted to support high bumblebee diversity. We identify areas where targeted searches may
18 reveal undiscovered populations of rare bumblebee species. Obtaining a good knowledge of the
19 current distribution of species is a vital first step towards devising approaches for their
20 conservation.

21
22 Keywords: Iberian bumblebees; mountains; undersampled; Maxent; climatic distribution

INTRODUCTION

Bumblebees (*Bombus* spp.) are important wild pollinators of many wild flowers and provide valuable services for agricultural crops (Corbet, 1987; Goulson, 2007). In the past decades many bumblebee species have declined with a number facing extinction in Europe, North America and Asia (Goulson et al., 2008; Williams and Osborne, 2009; Casey et al., 2015). Mainly due to human activities, these insects face multiple threats, including exposure to pesticides, habitat loss, introduction of non-native bees and their parasites, and climate change (Goulson et al., 2008; Whitehorn et al., 2012; Graystock et al., 2013; Ploquin et al., 2013).

The essential first step in devising conservation strategies for threatened species is to establish their distribution (Eken et al., 2004). Worldwide there are approximately 250 species of bumblebee, and knowledge of their distributions varies greatly between geographic regions: the north of Europe and the north of America represent well known regions whereas the south of Europe, South America and much of Asia still present large knowledge gaps. In fact, these gaps can correspond to undersampled areas, i.e. areas where certain species occur but which have not been surveyed.

The Iberian Peninsula corresponds to the south-west edge of bumblebees' distribution in Europe, and is thus a region where we might expect impacts of climate change to be significant (Thuiller, 2007). There are 38 species recognized for the entire Peninsula, which corresponds to ca. 60% of the European bumblebee fauna (Ortiz-Sánchez, 2011; Lecocq et al., 2011; Rasmont et al., 2015). However, there is little information on their ecology and distribution patterns (but see Ploquin et al., 2013). In the Iberian Peninsula the majority of literature on bumblebees merely lists records, mostly focusing in the north and east (e.g. Ornos, 1991; Castro, 1996). To our best knowledge, the only ecological studies regarding the bumblebee community were developed in the Cantabrian Mountains (northern Spain) (Obeso, 1992; Ploquin et al., 2013; Herrera et al., 2013). This lack of knowledge combined with the susceptibility for the rapid decline of marginal populations (Williams et al., 2009) highlight the urgency of studies on this southern European region.

Species distribution modeling (SDM) techniques are important tools to assess the potential geographic distribution of target species (Guisan and Zimmermann, 2000). This approach combines species' occurrence records with ecological meaningful variables (climate, habitat, topographic data, etc.) to identify which environmental conditions are required for the maintenance of populations (Pearson, 2007). In SDMs, the species data used can be presence-only, presence/absence or abundance data. Presence-only methods are especially appropriate

when false absences (the species was present although not detected) are likely to occur (Elith et al., 2006). For conservation biologists this method is a powerful tool that can help guide conservation-management strategies for invasive species (Kadoya et al., 2009), endangered species (Sousa-Silva et al., 2014) and species with uncertain distributions (Rebelo and Jones, 2010). These techniques are particularly useful for invertebrates for which distribution patterns are often poorly documented, since they can predict distributions based on sparse data (Bosso et al., 2013).

SDM techniques have recently been applied to bumblebees (Kadoya et al., 2009; Koch and Strange 2009; Herrera et al. 2013; Pradervand et al., 2014; Rasmont et al., 2015; Casey et al., 2015). For example, Kadoya et al. (2009) use this approach to predict the likely future distribution of the invading European *Bombus terrestris* in Japan. Rasmont et al. (2015) investigated the likely effects of climate change on bumblebee species at a European scale, predicting that most of the European bumblebee species will present range contractions, whereas four or five species could expand their ranges, and up to eleven species will not suffer changes. They also predict major reductions of suitable climatic space in southern Europe, particularly in the Iberian Peninsula (Rasmont et al., 2015).

The main goal of this study was to understand the spatial patterns of bumblebee diversity in Iberia Peninsula and Balearic archipelago while identifying the main priorities for future research and conservation. Therefore we present the following questions: a) How is bumblebee diversity spatially structured? b) Which areas possess larger knowledge gaps? c) Which bumblebee species are of potential concern? d) What are the main climatic factors shaping bumblebee distributions in Iberia?

MATERIALS AND METHODS

STUDY AREA

The area studied is located in south-western Europe and comprises the Iberia Peninsula (580 000 km²) and the Balearic archipelago (5 000 km²). The Iberian Peninsula was one of the most important Pleistocene glacial refugia in Europe (Hewitt, 1999). It contains a remarkable biological diversity (Blondel and Aronson, 1999) and a wide range of climatic and topographic conditions (Hagget, 2002). **The northern territory is humid and colder compared to the drier and warmer south (Hagget, 2002) and different mountainous systems (locally known as “Serras” or “Sierras”) are found mainly in the central and northern regions of the peninsula.** The climate includes Mediterranean, Atlantic, alpine, and some regions in the southeast are near desert

(Hagget, 2002). Two main biogeographical regions dominate the Peninsula: the Eurosiberian and the Mediterranean (Sillero et al., 2009).

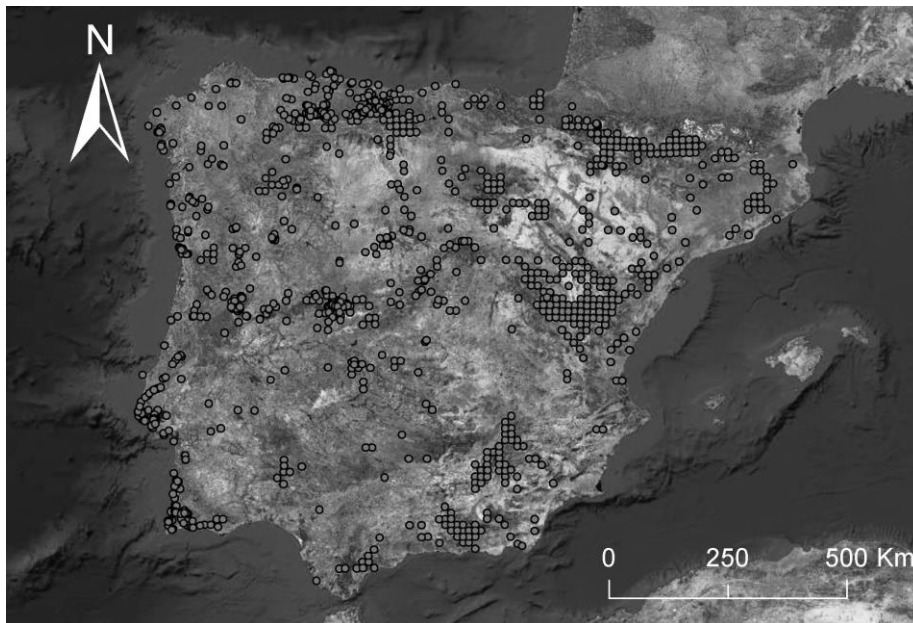


Fig. 1. The Iberian Peninsula and the Balearic archipelago with all the presence data collected. Map source: ArcGIS 10.1.

SPECIES DISTRIBUTION DATA

We compiled 5,795 records for 38 species (Fig.1) of which 5,409 (93%) were incorporated into the analysis according to criteria described below. The records used were compiled from different sources: 1) unpublished observations by the authors (122); 2) unpublished observations by other researchers and naturalists (4742); 3) observations found in published literature (491); 4) museum collections of the National Museum of Natural History and Science, Lisbon (54). The majority of the records (84%) are from within the last 35 years, and 51% are from the 1980's. The records that we used in this study are trustworthy, because they were identified by the most experienced bee researchers and experts on the Iberian bumblebee fauna. Records of doubtful accuracy were excluded.

Observations from *Bombus reinigiellus* (restricted to Sierra Nevada, Spain) and the cryptic *Bombus lucorum*-species complex were excluded (Williams et al., 2012a). Cryptic species might induce modeling bias resulting from incorrect identification. We also excluded three species that were represented by less than 11 records: *Bombus flavidus*, *Bombus gerstaeckeri* and *Bombus norvegicus* (Wisz et al., 2008). Data with lower accuracy than 10 km were also excluded. We attributed the records to a grid of 10 x 10 km cells, removing duplicates

so that within each cell there was only one record for each species. In order to remove the spatial autocorrelation from each species, we calculated the climatic heterogeneity layer for rarefying data with the multi-distance option in “SDMtoolbox” (Brown, 2014) of ArcMap GIS. After these processes we were left with 1,807 records for 32 species.

ECOGEOGRAPHICAL VARIABLES

A set of variables with 5 arc-minutes resolution (ca. 10 km) were obtained from WorldClim (www.worldclim.org) to calculate bio-climatic variables that are biological meaningful for bumblebees, from February to October. We defined this interval because it corresponds to the period of activity for most of the species according to the dates in our list of records. ArcGIS 10.1 (ESRI, 2013) was used to calculate the bioclimatic variables and to clip them to the study area. The nine variables produced were: mean temperature, mean diurnal range, maximum temperature of the warmest month, minimum temperature of coldest month, temperature range, total precipitation, precipitation of wettest month, precipitation of driest month and altitude. We defined 10 x 10 km as the spatial resolution to do the model calculations, as otherwise many records of low precision would have had to be discarded. This resolution is too large to capture local effects of habitat and topography on bumblebee distribution patterns, so these were not included in the analysis (Pearson and Dawson 2003). We tested multicollinearity of the variables and retained only one from each group of variables with correlations higher than 0.8 (Elith et al. 2010). Within a group of correlated variables we retained the one that achieved a higher likelihood with species’ distribution in univariate Maxent models (see below for Maxent procedure). Thus, altitude (which was closely correlated with annual mean temperature) and temperature annual range (which was closely correlated with mean diurnal range) were excluded from subsequent analyses.

MODELLING PROCEDURE AND GIS ANALYSES

SDMs were developed using a maximum entropy modeling technique, as available in the software Maxent version 3.3.3k (Phillips et al., 2006). This technique has become very popular and is widely accepted as the approach with one of the best performances among other techniques for SDMs (Elith et al., 2006; Elith et al., 2011). It has the advantage of using presence-only data and has good performances with small sample sizes (Wisz et al., 2008).

We imported into Maxent seven climatic variables (independent variables) and autocorrelation-free species presence records (dependent variables). We set the regularization

multiplier of 2 and ran 5 equal-sized partitions using cross-validation, in which the whole presence data is geographically split. The area under the curve (AUC) of the receiver operating characteristics (ROCs) plot was taken as a measure of models performance (Fielding and Bell, 1997). AUC can be interpreted as follows: excellent (0.90–1.00), very good (0.8–0.9), good (0.7–0.8), fair (0.6–0.7), and poor (0.5–0.6) (Swets, 1988). The species response curves were also calculated to determine the effect of each variable on the species occurrence (Baldwin, 2009). The models were classified using the “reclassify” function in ArcMap GIS into presence–absence through the maximum training sensitivity plus specificity logistic threshold value (Liu et al., 2013). Predicted hot-spots were calculated by summing the model results (predicted maps) in the “raster calculator” function in ArcMap GIS. We created a buffer of 50 km in ArcMap GIS using the species observed data to extend the distribution data in order to assume an entire region as a true presence. The potential undersampled areas were estimated through the difference between those buffers and the predicted results (gap analysis).. The shape files of protected areas in the Iberian Peninsula were obtained from the Institute for the Conservation of Nature and Forest - ICNF (Portugal) and EUROPARC (Spain) in order to calculate the percentage of suitable climatic habitat in protected areas for each species.

RESULTS

The percentage of predicted area climatically suitable for each species (prevalence) in the Iberian Peninsula and Balearic archipelago was calculated with the reclassified models (Table 1). Thereafter, we used prevalence to classify species into three groups aggregated according to their potential area of occurrence: 1) widespread species with climatically suitable areas covering most of the study area (prevalence > 30%); 2) regional species with large areas climatically suitable, but highly fragmented (10% < prevalence < 30%); 3) restricted species with smaller and confined climatically suitable areas (prevalence < 10%) (Table 1).

MODELS PERFORMANCE AND VALIDATION

The ROC plots for the training dataset for regional and restricted species exhibited an average $AUC_{\text{trains}} \geq 0.9$ and widespread species had an average $AUC_{\text{trains}} \geq 0.7$. The average test AUCs were slighter lower thus showing that the models did not suffer from overfitting. Only for one species, *B. terrestris*, did the model performance change from good to fair ($AUC_{\text{test}} = 0.66$).

SPECIES DISTRIBUTION: HOT-SPOTS AND UNDERSAMPLED AREAS

Prevalence of bumblebee species varied from 73% for the very widespread *B. terrestris* to less than 5% for ten of the restricted species, with the montane specialist *Bombus pyrenaicus* having the lowest prevalence of all (0.83%) (Table 1). The hot-spots for the bumblebees in the Iberian Peninsula and Balearic archipelago are located mostly in mountain ranges in the north (Cantabrian Mountains and Pyrenees) and in the north-center of the Peninsula (Iberian Central System and Iberian System) (Fig. 2, 3). In the south, the Sierra Nevada which has the highest peak of the peninsula was also highlighted by the models as being rich in species. The hot-spots of restricted and regional species are concentrated mainly in the northern mountains whereas widespread species hot-spots expand from high altitude (mountains) into low altitude areas surrounding those mountain chain ranges.

Overall, there are potentially large undersampled areas for bumblebees in the study area (Fig. 4). They are mainly located in the west of the Peninsula in Portugal and Galicia (Spain), in the south of the Cantabrian Mountains, the Pyrenees and its surroundings, in the Iberian Central System and in vast areas of the south. The undersampled areas for restricted species are located in the Pyrenees and its surroundings, some parts of Iberian System, Galicia and the Iberian Central System. The Serra da Estrela (Portugal) which belongs to the Iberian Central System and the Sierra Nevada are isolated undersampled areas. Looking at the species level, the wide-spread *Bombus vestalis* had the largest undersampled area (72%) and the restricted *B. pyrenaicus* had the lowest (3%) (Table 1). Several other species presented large undersampled areas (> 40%). This was the case for the widespread *Bombus muscorum*, the regional *Bombus cullumanus*, *Bombus barbutellus*, *Bombus campestris*, *Bombus confusus* and the restricted *Bombus mendax*, *Bombus quadricolor*, *Bombus subterraneus* and *Bombus inexpectatus*. In contrast, two restricted species presented low prevalence together with small undersampled areas: *Bombus soroeensis* and *B. pyrenaicus* (Table 1).

The percentage of climatically suitable area covered by protected areas was highest for restricted species (30% < range < 53%), whereas widespread species had the lowest percentage (15% < range < 18%). Looking at the species level, the widespread *B. terrestris* had the lowest area covered by protected areas (15%) and the restricted *B. pyrenaicus* had the largest (61%) (Table 1).



Fig. 2. Topographical map of the Iberian Peninsula and the Balearic archipelago with hot-spots for bumblebees marked. Map source: QGIS 2.6.1.

IMPORTANCE OF CLIMATIC VARIABLES FOR SPECIES DISTRIBUTION

The most important climatic variables shaping the bumblebee distribution in the Iberian Peninsula and Balearic archipelago were mean temperature and maximum temperature of the warmest month, which were selected for 31 and 30 species respectively (Table 1). When considering the responses curves profiles of those variables they show an overall negative response of bumblebees to increasing temperature. When sorted by groups, widespread species show higher climatic tolerance to temperature increases than regional and restricted species (Fig. 5). The average probability of presence with respect to mean temperature is zero at approximately 14°C for restricted, 17°C for regional and 20°C for widespread species. Following the same pattern, the average probability of presence in maximum temperature of the warmest month is zero at 27.5°C in restricted, 32°C for regional and 35°C for widespread species WSP. Minimal temperature of coldest month and precipitation of driest month were the following most selected variables (for 16 species each), whereas precipitation, mean diurnal range and precipitation of the wettest month were important for one species alone.

DISCUSSION

In this study we explore for the first time the climatic conditions that explain the distribution of Iberian bumblebees and we observed the following: 1) restricted and regional species are climatic specialist species that inhabit mountain regions; 2) widespread species are more tolerant of a broader range of climates, notably of higher temperatures; 3) some areas of Iberia are largely undersampled, including areas predicted to harbor a rich community of bumblebees (e.g. Serra da Estrela and Sierra Nevada) ; 4) one-third of species are clearly undersampled.

Bumblebees are generally intolerant of hot and dry environments (Iserbyt and Rasmont, 2012). Therefore, they tend to be more diverse in mountain ranges (Williams et al., 2010; Ploquin et al., 2013) where many species are found actively foraging at high altitudes (Dillon and Dudley, 2014). Mountains coincide with the Eurosiberian biogeographical region in our study area (Sillero et al., 2009), characterized by a milder and more humid climate than is found in the remainder of the Iberian Peninsula. Not surprisingly, the distribution patterns of restricted and regional species were strongly associated with this biogeographical region. On the other hand, widespread species were found in both Mediterranean and Eurosiberian biogeographical regions. However, most species are absent from the hottest and driest areas of the Mediterranean zone. The distribution patterns are supported by response curves of mean temperature and maximum temperature of the warmest month which show a gradient of climatic tolerance: regional and restricted species with a high marginality and a low temperature tolerance correspond to Atlantic species, whereas widespread species have a lower marginality and higher temperature tolerance compared to the other two groups. Therefore, as Atlantic species exploit environments with average low temperatures they behave as specialist species, in contrast to widespread species that tend to be more tolerant of high temperatures (Peers et al., 2012).

Traditionally, the distinction between specialists and generalists among bumblebees has been defined according to the exploitation of food resources (Lavery and Plowright, 1988; Thostesen and Olesen, 1998; Goulson et al., 2005). Despite bumblebees being considered to be generalist foragers, some bumblebee species have narrower diet niches than others. For example, *Bombus consobrinus* forages mainly in *Aconitum* spp. (Thostesen and Olesen, 1998). In this study, we contrasted the specialist versus generalist status according to the climatic niche exploitation. Iberian bumblebees span a broad range of climatic tolerances, though most of the species (restricted and regional species) fall into the specialist category, at least within the range of climates found in Iberia (Sillero et al., 2009).

Although several faunal and floral studies follow the classical Eurosiberian-Mediterranean biogeographical pattern in the Iberian Peninsula and the Balearic archipelago (i.e. Carrascal and Lobo, 2003; Rueda et al., 2010), other studies do not support the same

division (García-Barros et al., 2002; Moreno Saiz et al., 2013(Moreno Saiz et al., 2013)). For example, Carrascal and Lobo (2003) show that birds' diversity is high in Eurosiberian regions whereas analyses by Moreno Saiz et al. (2013) did not support the Eurosiberian–Mediterranean division for vascular plants. The results presented in this study partly support the classical division. Only widespread species seem to span both biogeographical regions.

The study area is at the edge of the latitudinal range for most of the Iberian bumblebee fauna, which can only survive in habitats with average low temperatures. Therefore, taking into consideration the climatic change forecasts for Iberia into warmer and drier conditions (Thuiller, 2007; Giorgio and Lionello, 2007), many of the bumblebee species can expect their distribution ranges to shrink or even disappear (William and Osborne, 2009; Rasmont et al., 2015). The several isolated mountains in the centre and south of the Peninsula (for example the Serra da Estrela and Sierra Nevada) may function as refugees for bumblebees in those hotter climatic scenarios (Giorgio and Lionello, 2007).

Mountains are rich ecosystems and due to its importance many of them are classified as protected areas all over the globe (IUCN, 2004). In Iberia, the majority of protected areas occur in the mountains (ICNF, 2015; EUROPARC, 2015) and these regions are historically less affected by human activity than the lowlands. As a result, restricted bumblebee species in Iberia tend to have higher proportions of their range within protected areas (~30-60%), which is reassuring from a conservation perspective.

According to the IUCN red list of threatened species there are seven species among the 32 included in our analyses that have less favorable conservation status (Table 1). *Bombus cullumanus* is listed with threatened conservation status (Ornosa and Ortiz-Sánchez, 2011; Nieto et al., 2014) and it is widely believed that might be extinct in most of Europe, despite being common in parts of its Asian range (Kosior et al., 2007; Williams et al., 2012b). One of the last recent records in Europe for this species was in the Pyrenees (Ornosa and Ortiz-Sánchez, 2011) and together with the Massif Central of France these are the last known locations for this species in Europe (Rasmont and Iserbyt, 2013). According to our results a large area is still undersampled for *B. cullumanus*, and so it is possible that populations of this species remain undiscovered. Other species that have less favourable conservation status also present large undersampled areas, notable *B. muscorum* (widespread), *B. confusus* (regional), *B. inexpectatus* (restricted) and *B. mendax* (restricted) (Ornosa, 2011; Ornosa and Torres, 2011a; Ornosa and Torres, 2011b; Nieto et al., 2014). With the possible exception of *B. muscorum*, these three species are thought to have declined in recent decades in Iberia, and few populations have been recently confirmed (Ornosa, 2011; Ornosa and Torres, 2011a; Ornosa and Torres,

2011b). To clarify their current range it would be necessary to increase sampling effort in their undersampled areas (see supplementary material), and to revisit sites where they have not been recorded for many years. Interestingly, *B. muscorum* is the only species with a concerning conservation status that is still relatively common in Iberia. However, it has been predicted that, under likely future climate change scenarios, this species may become extinct in Iberia (Rasmont et al., 2015).

This study has a significant limitation regarding the spatial scale used: it considers the distribution patterns of bumblebees at larger scales (i.e. 10 km x 10km). Therefore only the abiotic conditions were analysed rather than other factors such as habitat characteristics or historical factors that are important to determine species distributions at finer scales (Pearson and Dawson, 2003). Regardless of climate, species will not be present in sites if suitable habitat is not present, for example if it has been removed by man's activities (Westphal et al., 2003). Nevertheless, the results presented are robust in predicting broad spatial patterns of bumblebees. Regarding cuckoo bumblebees, they were not excluded from modelling analysis. These bees are dependent on their hosts, but climatic factors can also play a major role in influencing their distributions (Saino et al., 2009; Møller et al., 2011).

CONCLUSIONS

We identify the most biodiverse areas for Iberian bumblebees, and also identify many areas in need of increased sampling effort where rare species might be present. Our results should encourage conservationists and environmental agencies to focus surveys of these important pollinators on undersampled areas in order to inform conservation plans. In addition to improving our knowledge of the current distributions of bumblebees in Iberia, there is a need for further ecological studies since there is a paucity of information on the habitat requirements of Iberian bees. With the prospect of climate change impacting on populations which are already near their climatic limits in Iberia, the preservation of high quality habitats in the mountains may be the most efficient strategy for the conservation of Iberian bumblebees.

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REFERENCES

- Baldwin, R.A., 2009. Use of maximum entropy modeling in wildlife research. *Entropy* 11, 854–866.
- Blondel, J., Aronson, J., 1999. *Biology and wildlife of the Mediterranean region*. Oxford University Press, Oxford.

Bosso, L., Rebelo, H., Garonna, A.P., Russo, D., 2013. Modelling geographic distribution and detecting conservation gaps in Italy for the threatened beetle *Rosalia alpina*. *J. Nat. Conserv.* 21, 72–80.

Brown J.L., 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic, and species distribution model analyses. *Methods in Ecology and Evolution*.

Carrascal, L.M., Lobo, J.M., 2003. Respuestas a viejas preguntas con nuevos datos: estudio de los patrones de distribución de la avifauna española y consecuencias para su conservación. In *Atlas de las aves reproductoras de España*, 651–668.

Casey, L.M., Rebelo, H., Rotheray, E., Goulson, D., 2015. Evidence for habitat and climatic specializations driving the long-term distribution trends of UK and Irish bumblebees. *Divers. Distrib.* 1-12.

Castro, L., 1996. Catalogus 9. Insecta: Hymenoptera 1. *Cat. Entomofauna Aragon.* 9, 3-6.

Corbet, S.A., 1987. More bees make better crops. *New Scientist.* 115, 40–43.

Dillon, M.E., Dudley, R., 2014. Surpassing Mt. Everest: extreme flight performance of alpine bumble-bees. *Biol. Lett.* 10, 20130922.

Eken, G., Bennun, L., Brooks, T.M., Darwall, W., Fishpool, L.D.C., Foster, M., Knox, D., Langhammer, P., Matiku, P., Radford, E., Salaman, P., Sechrest, W., Smith, M.L., Spector, S., Tordoff, A., 2004. Key Biodiversity Areas as Site Conservation Targets. *Bioscience* 54, 1110.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, a., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, a., Li, J., Lohmann, L.G., Loiselle, B. a., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Peterson, a. T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, S.M., Zimmermann, E.N., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography.* 29, 129-151.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. *Methods Ecol. Evol.* 1, 330–342.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17, 43–57.

ESRI., 2013. ArcGis 10.1. Redlands, CA: Environmental Systems Research Institute, Inc.

EUROPARC-España. 2015. <http://www.redeuroparc.org/> accessed in January 2015.

Fielding, A.H; Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation* 24, 38–49.

García-Barros, E., Gurrea, P., Lucíañez, M.J., Cano, J.M., Munguira, M.L., Moreno, J.C., Sainz, H., Sanz, M.J., Simón, J.C., 2002. Parsimony analysis of endemism and its application to animal and plant geographical distribution in the Ibero-Balearic region (western Mediterranean). *J. Biogeogr.* 29, 109–124.

Giorgi, F., Lionello, P., 2007. Climate change projections for the Mediterranean region. *Glob. Planet. Change* 63, 90–104.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. *Biol. Conserv.* 122, 1–8.

Goulson, D., 2007. Bumblebees and other pollinating insects, in: Winspear, R. (Ed.), *The Farm and Wildlife Handbook*. RSPB, Sandy, pp. 105-112.

Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumblebees. *Annual Review of Entomology* 53, 191-208.

Goulson, D., 2010. *Bumblebees: their behaviour, ecology and conservation*, second ed. Oxford University Press, Oxford.

- Graystock, P., Yates, K., Evison, S.E.F., Darvill, B., Goulson, D., Hughes, W.O.H., 2013. The Trojan hives: pollinator pathogens, imported and distributed in bumblebee colonies. *Journal Applied Ecology*.
- Guisan, A., Zimmerman, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* 135, 147–186.
- Herrera, J.M., Ploquin, E.F., Rodríguez-Pérez, J., Obeso, J.R., 2013. Determining habitat suitability for bumblebees in a mountain system: A baseline approach for testing the impact of climate change on the occurrence and abundance of species. *J. Biogeogr.* 41, 700–712.
- Hagget, P., 2002. *Encyclopedia of World Geography. Spain and Portugal*. Marshall Cavendish Corporation.
- Hewitt, G.M., 1999. Post-glacial re-colonization of European biota. *Biol. J. Linn. Soc.* 68, 87–112.
- ICNF. 2015. <http://www.icnf.pt/> accessed in January 2015.
- Iserbyt, S., Rasmont, P., 2012. The effect of climatic variation on abundance and diversity of bumblebees: A ten years survey in a mountain hotspot. *Ann. la Soc. Entomol. Fr.* 48, 261–273.
- IUCN. 2004. *Guidelines for Planning and Managing Mountain Protected Areas*. IUCN, Gland, Switzerland and Cambridge, UK. xi + 83pp.
- Kadoya, T., Ishii, H.S., Kikuchi, R., Suda, S.I., Washitani, I., 2009. Using monitoring data gathered by volunteers to predict the potential distribution of the invasive alien bumblebee *Bombus terrestris*. *Biol. Conserv.* 142, 1011–1017.
- Koch, J.B., Strange, J.P., 2009. Constructing a species database and historic range maps for North American Bumblebees (*Bombus sensu stricto* Latreille) to inform conservation decisions. *Uludag Bee Journal* 9, 97–108.

- Kosior, A., Celary, W., Olejniczak, P., Fijal, J., Król, W., Solarz, W., Plonka, P., 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx* 41, 79.
- Laverty, T.M., Plowright, R.C., 1988. Flower handling by bumblebees: a comparison of specialists and generalists. *Anim. Behav.* 36, 733–740.
- Lecocq, T., Lhomme, P., Michez, D., Dellicour, S., Valterová, I., Rasmont, P., 2011. Molecular and chemical characters to evaluate species status of two cuckoo bumblebees: *Bombus barbutellus* and *Bombus maxillosus* (Hymenoptera, Apidae, Bombini). *Syst. Entomol.* 36, 453–469.
- Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40, 778–789.
- Møller, A.P., Saino, N., Adamík, P., Ambrosini, R., Antonov, A., Campobello, D., Stokke, B.G., Fossøy, F., Lehikoinen, E., Martin-Vivaldi, M., Moksnes, A., Moskat, C., Røskaft, E., Rubolini, D., Schulze-Hagen, K., Soler, M., Shykoff, J.A., 2011. Rapid change in host use of the common cuckoo *Cuculus canorus* linked to climate change. *Proc. Biol. Sci.* 278, 733–738.
- Moreno Saiz, J.C., Donato, M., Katinas, L., Crisci, J. V., Posadas, P., 2013. New insights into the biogeography of south-western Europe: Spatial patterns from vascular plants using cluster analysis and parsimony. *J. Biogeogr.* 40, 90–104.
- Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Quaranta, M., Radchenko, V.G., Scheuchl, E., Smit, J., Straka, J., Terzo, M., Tomozii, B., Window, J. and Michez, D., 2014. European Red List of bees. Luxembourg: Publication Office of the European Union.
- Obeso, J.R., 1992. Geographic distribution and community structure of bumblebees in the northern Iberian peninsula 89, 244–252.

Ornosa, C., 1991. Consideraciones taxonómicas sobre el subgénero *Megabombus* Dalla Torre, 1880, en la Península Ibérica (Hym., Apidae, Bombinae). *Anales de Biología*, 33-41.

Ornosa, C., 2011. *Bombus confusus* (Schenck, 1861). Pp: 1174-1178. In: Verdú, J.R., Numa, C., Galante, E. (Eds). *Atlas y Libro Rojo de los Invertebrados amenazados de España (Especies Vulnerables)*. Dirección General de Medio Natural y Política Forestal, Ministerio de Medio Ambiente, Medio rural y Marino, Madrid.

Ornosa, C., Ortiz-Sánchez, F.J., 2011. *Bombus cullumanus* (Kirby, 1802). Pp: 408-411. In: Verdú, J.R., Numa, C., Galante, E. (Eds). *Atlas y Libro Rojo de los Invertebrados amenazados de España (Especies Vulnerables)*. Dirección General de Medio Natural y Política Forestal, Ministerio de Medio Ambiente, Medio rural y Marino, Madrid.

Ornosa, C., Torres, F., 2011a. *Bombus inexpectatus* (Tkalcu° 1963). Pp: 417-421. In: Verdú, J.R., Numa, C., Galante, E. (Eds). *Atlas y Libro Rojo de los Invertebrados amenazados de España (Especies Vulnerables)*. Dirección General de Medio Natural y Política Forestal, Ministerio de Medio Ambiente, Medio rural y Marino, Madrid.

Ornosa, C., Torres, F., 2011b. *Bombus mendax* (Gerstaecker, 1869). Pp: 417-421. In: Verdú, J.R., Numa, C., Galante, E. (Eds). *Atlas y Libro Rojo de los Invertebrados amenazados de España (Especies Vulnerables)*. Dirección General de Medio Natural y Política Forestal, Ministerio de Medio Ambiente, Medio rural y Marino, Madrid.

Ortiz-Sánchez, F.J., 2011. Lista actualizada de las especies de abejas de España (Hymenoptera: Apoidea: Apiformes). *Boletín de la Sociedad Entomológica Aragonesa*. 49, 265–281.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371.

Pearson, R.G., 2007. Species' distribution modeling for conservation educators and practitioners. Synthesis. American Museum of Natural History: <http://ncep.amnh.org>.

- Peers, M.J.L., Thornton, D.H., Murray, D.L., 2012. Reconsidering the Specialist-Generalist Paradigm in Niche Breadth Dynamics: Resource Gradient Selection by Canada Lynx and Bobcat. PLoS One 7.
- Phillips S.J., Anderson R.P., Schapire R., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231–259.
- Ploquin, E., Herrera, J.M. & Obeso, J.R., 2013. Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. Oecologia.
- Pradervand, J.-N., Pellissier, L., Randin, C.F., Guisan, A., 2014. Functional homogenization of bumblebee communities in alpine landscapes under projected climate change. Clim. Chang. Responses. 1, 1.
- Rasmont P., Iserbyt I., 2013. Atlas of the European Bees: genus *Bombus*. 3d Edition. STEP Project, Atlas Hymenoptera, Mons, Gembloux.
<http://www.zoologie.umh.ac.be/hymenoptera/page.asp?ID=169>
- Rasmont P., Franzén M., Lecocq T., Harpke A., Roberts S.P.M., Biesmeijer J.C., Castro L., Cederberg B., Dvůrák L., Fitzpatrick Ú., Gonthier Y., Haubruge E., Mahé G., Manino A., Michez D., Neumayer J., Ødegaard F., Paukkunen J., Pawlikowski T., Potts S.G., Reemer M., J. Settele, J. Straka, Schweiger O., 2015. Climatic Risk and Distribution Atlas of European Bumblebees. Biorisk 10 (Special Issue), 246 pp.
- Rebelo, H., Jones, G., 2010. Ground validation of presence-only modelling with rare species: a case study on barbastelles *Barbastella barbastellus* (Chiroptera: Vespertilionidae). Journal of Applied Ecology. 47, 410–420.
- Rueda, M., Rodríguez, M.Á., Hawkins, B.A., 2010. Towards a biogeographic regionalization of the European biota. J. Biogeogr. 37, 2067–2076.
- Sillero, N., Brito, J.C., Skidmore, A.K., Toxopeus, A.G., 2009. Biogeographical patterns derived from remote sensing variables: the amphibians and reptiles of the Iberian Peninsula. Amphibia-Reptilia 30, 185–206.

573

574 Saino, N., Rubolini, D., Lehikoinen, E., Sokolov, L. V, Bonisoli-Alquati, A., Ambrosini, R.,
 575 Boncoraglio, G., Møller, A.P., 2009. Climate change effects on migration phenology may
 576 mismatch brood parasitic cuckoos and their hosts. *Biol. Lett.* 5, 539–541.

577

578 Sousa-Silva, R., Alves, P., Honrado, J., Lomba, A., 2014. Improving the assessment and
 579 reporting on rare and endangered species through species distribution models. *Glob. Ecol.*
 580 *Conserv.* 2, 226–237.

581

582 Swets J.A., 1988. Measuring the accuracy of diagnostic systems. *Science.* 240, 1285–1293.

583

584 Thostesen, A.M., Olesen, J.M., 1996. Pollen removal and deposition by specialist and generalist
 585 bumblebees in *Aconitum septentrionale*. *Oikos.* 77, 77–84.

586

587 Thuiller, W., 2007. Biodiversity: climate change and the ecologist. *Nature.* 448, 550–552.

588

589 Verdú, J.R., Numa, C., Galante, E. (Eds) 2011. Atlas y Libro Rojo de los Invertebrados
 590 amenazados de España (Especies Vulnerables). Dirección General de Medio Natural y Política
 591 Forestal, Ministerio de Medio Ambiente, Medio rural y Marino, Madrid, 1.318 pp.

592

593 Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2003. Mass flowering crops enhance
 594 pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961–965.

595

596 Whitehorn, P.R., O’Connor, S., Wackers, F.L., Goulson, D., 2012. Neonicotinoid pesticide
 597 reduces bumblebee colony growth and queen production. *Science.* 336: 351-352.

598

599 Williams, P.H., Colla, S., Xie, Z., 2009. Bumblebee vulnerability: Common correlates of
 600 winners and losers across three continents. *Conserv. Biol.* 23, 931–940.

601

602 Williams, P.H., Osborne, J.L., 2009. Bumblebee vulnerability and conservation world-wide.
 603 *Apidologie* 40, 367–387.

604

605 Williams, P.H., Ito, M., Matsumura, T., Kudo, I., 2010. The bumblebees of the Nepal Himalaya
 606 (Hymenoptera:Apidae). *Insecta Matsumurana.* 66, 115-151.

607

608 Williams, P.H., Brown, M.J.F., Carolan, J.C., An, J., Goulson, D., Aytekin, a. M., Best, L.R.,
609 Byvaltsev, A.M., Cederberg, B., Dawson, R., Huang, J., Ito, M., Monfared, A., Raina, R.H.,
610 Schmid-Hempel, P., Sheffield, C.S., Sima, P., Xie, Z., 2012a. Unveiling cryptic species of the
611 bumblebee subgenus *Bombus* s. str. worldwide with COI barcodes (Hymenoptera: Apidae) 37–
612 41.

613

614 Williams, P.H, Byvaltsev, A., Sheffield, C., Rasmont, P., 2012b. *Bombus cullumanus* - an
615 extinct European bumblebee species? *Apidologie*.

616

617 Wisz, M.S., Hijmans, R.J., Li, J., Peterson, a. T., Graham, C.H., Guisan, a., Elith, J., Dudík, M.,
618 Ferrier, S., Huettmann, F., Leathwick, J.R., Lehmann, a., Lohmann, L., Loiselle, B. a., Manion,
619 G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Phillips, S.J., Richardson, K.S.,
620 Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S.E., Zimmermann, N.E., 2008.
621 Effects of sample size on the performance of species distribution models. *Divers. Distrib.* 14,
622 763–773.

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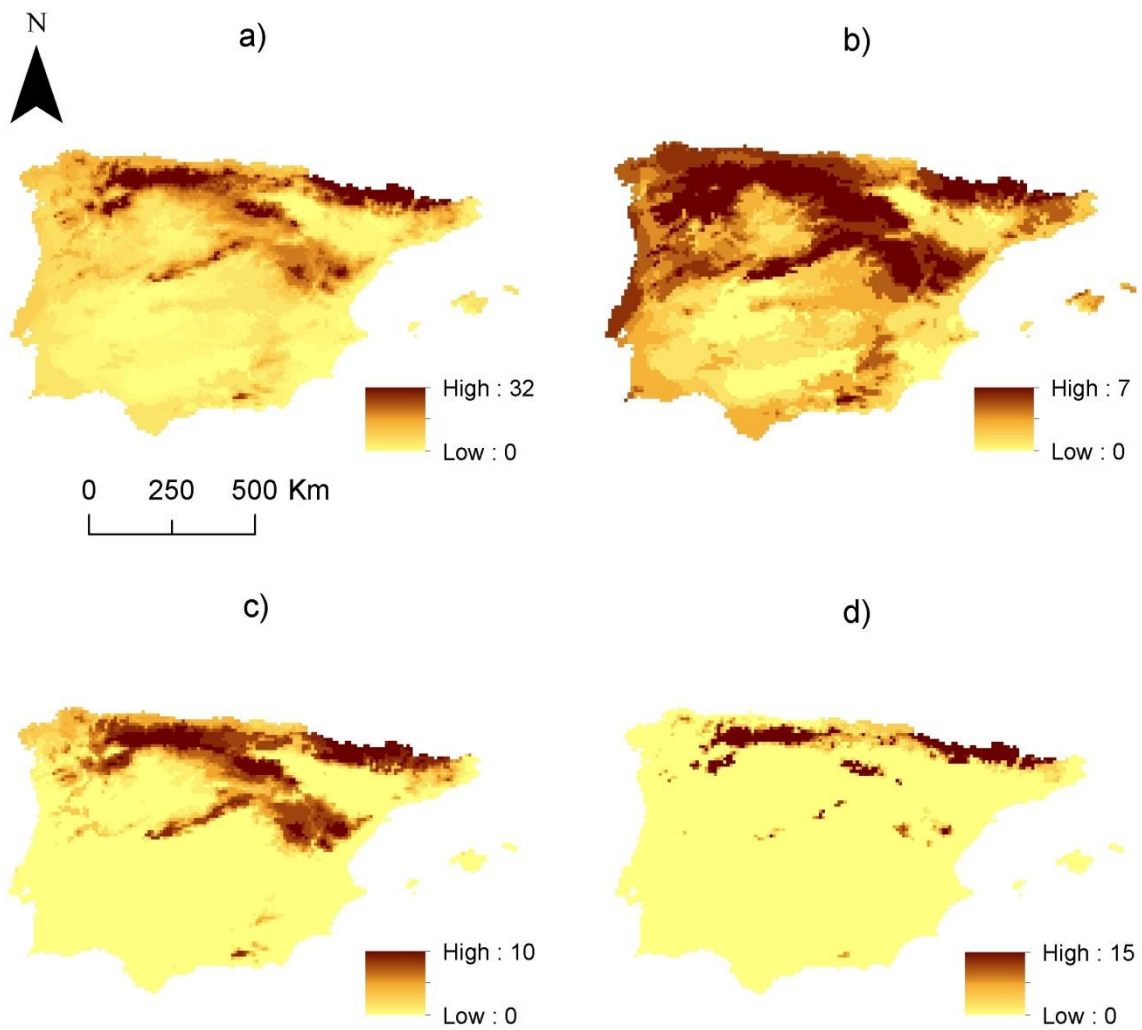
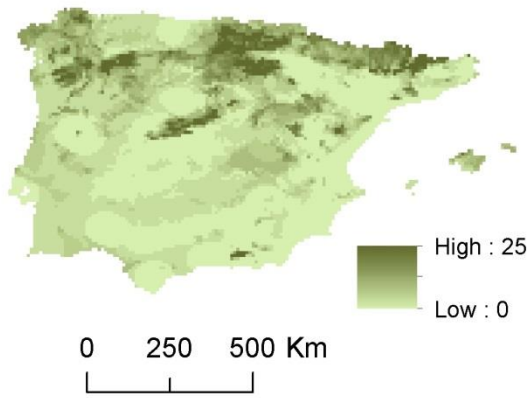


Fig.3. Species richness maps of the Iberian Peninsula and the Balearic archipelago for **a)** Total bumblebee (BB) species; **b)** wide-spread BB species; **c)** regional distributed BB species; **d)** restricted BB species. Darker areas indicate higher species richness.

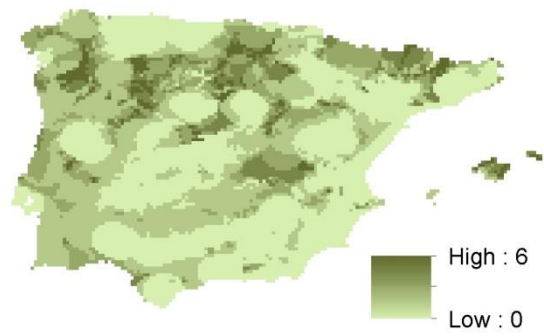
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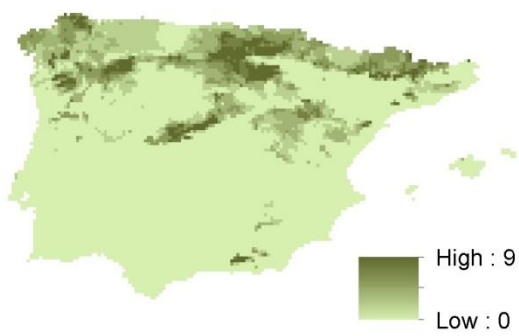
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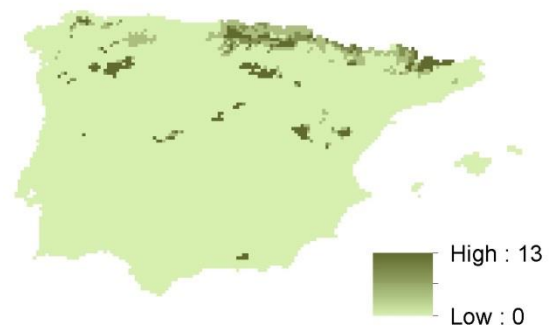
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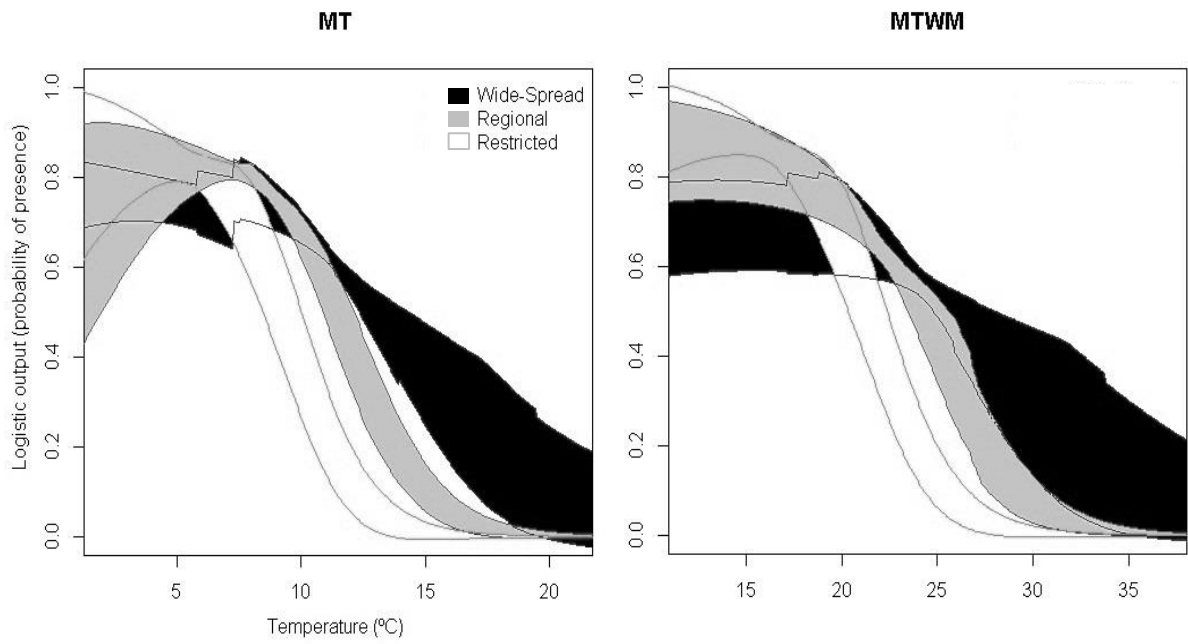


Fig.5. Average environmental response curves (with standard deviation shown) for a) Mean temperature and b) Maximum temperature of the warmest month.

678 **Table.1.** List for the 32 bumblebee species regarding: a) **percentage of prevalence**; b)
679 **percentage of undersampled area**, c) **percentage of protected areas**; d) **IUCN status** (LC-
680 least concern; **VU**-vulnerable; **CR** – critically endangered; **EN** – endangered; **NT** - Near
681 Threatened; e) **climatic variables** following an importance order for each species (**MTCM** -
682 Min Temperature Coldest Month; **MT** - Mean Temperature; **MTWM** - Max Temperature
683 Warmest Month; **MDR** - Mean Diurnal Range; **PWM** - Precipitation Wettest Month; **PDM** -
684 Precipitation Driest Month; **P** - Precipitation. (*)- Species with less favorable conservation
685 status with their status in bold.

Species	Prevalence (%)	Undersampled (%)	Protected áreas (%)	IUCN status (*)	Spanish red list	1 st variable	2 nd variable	3 rd variable
WIDE-SPREAD SPECIES								
<i>B. terrestris</i>	73.42	9.76	15.21	LC	-	MTCM	MTWM	MT
<i>B. ruderatus</i>	59.53	17.48	16.03	LC	-	MTCM	MT	MTWM
<i>B. vestalis</i>	59.08	71.73	17.29	LC	-	MTCM	MT	PWT
<i>B. pascuorum</i>	47.56	9.96	16.91	LC	-	MT	MTWM	PDM
<i>B. muscorum</i>	36.19	47.14	15.44	VU	-	MT	MTWM	PDM
<i>B. pratorum</i>	35.24	31.52	18.46	LC	-	MT	MTCM	PDM
<i>B. hortorum</i>	34.47	8.51	18.39	LC	-	MTWM	MT	MDR
REGIONAL SPECIES								
<i>B. cullumanus</i>	25.75	54.59	19.62	CR	VU	MT	PDM	MTWM
<i>B. barbutellus</i>	25.45	46.13	21.26	LC	-	MT	MTCM	MTWM
<i>B. humilis</i>	24.76	20.94	18.95	LC	-	MT	MTWM	PDM
<i>B. lapidarius</i>	23.61	11.05	22.25	LC	-	MT	MTCM	MTWM
<i>B. sylvarum</i>	20.83	8.23	19.89	LC	-	PDM	MT	MTWM
<i>B. campestris</i>	20.27	57.29	23.26	LC	-	MTWM	MT	PDM
<i>B. mocsaryi</i>	18.43	34.51	15.92	EN	-	MTCM	MT	MTWM
<i>B. sylvestris</i>	17.17	39.92	23.81	LC	-	MT	MTWM	MTCM
<i>B. confusus</i>	16.04	64.25	22.42	VU	EN	PDM	MTWM	P
<i>B. rupestris</i>	11.23	15.95	28.81	LC	-	MT	MTCM	MTWM
RESTRICTED SPECIES								
<i>B. hypnorum</i>	9.26	30.71	30.35	LC	-	PDM	MTWM	MT
<i>B. ruderarius</i>	7.81	13.06	36.01	LC	-	MT	MTWM	PDM
<i>B. wurflenii</i>	7.56	37.93	35.26	LC	-	MT	MTWM	PDM

<i>B. jonellus</i>	5.97	28.14	37.52	LC	-	MT	PDM	MTWM
<i>B. mesomelas</i>	5.7	16.5	41.06	LC	-	MT	MTWM	MTCM
<i>B. mendax</i>	5.05	44.35	38.14	NT	EN	MTWM	MT	PDM
<i>B. bohemicus</i>	4.94	24.94	42.86	LC	-	MT	MTWM	MTCM
<i>B. soroensis</i>	4.94	7.71	43.08	LC	-	MT	MTWM	PDM
<i>B. quadricolor</i>	4.85	42.26	44.8	LC	-	MT	MTWM	MTCM
<i>B. subterraneus</i>	4.6	40.39	46.23	LC	-	MT	MTWM	MTCM
<i>B. sichelii</i>	3.88	18.79	48.84	LC	LC	MT	MTWM	PDM
<i>B. monticola</i>	2.74	17.96	49.39	LC	-	MT	MTWM	MTCM
<i>B. inexpectatus</i>	2.4	41.59	50.93	EN	VU	MT	MTWM	MTCM
<i>B. mucidus</i>	2.35	27.14	52.86	NT	-	MT	MTWM	MTCM
<i>B. pyrenaicus</i>	0.83	2.7	60.81	LC	-	PDM	MTWM	MT

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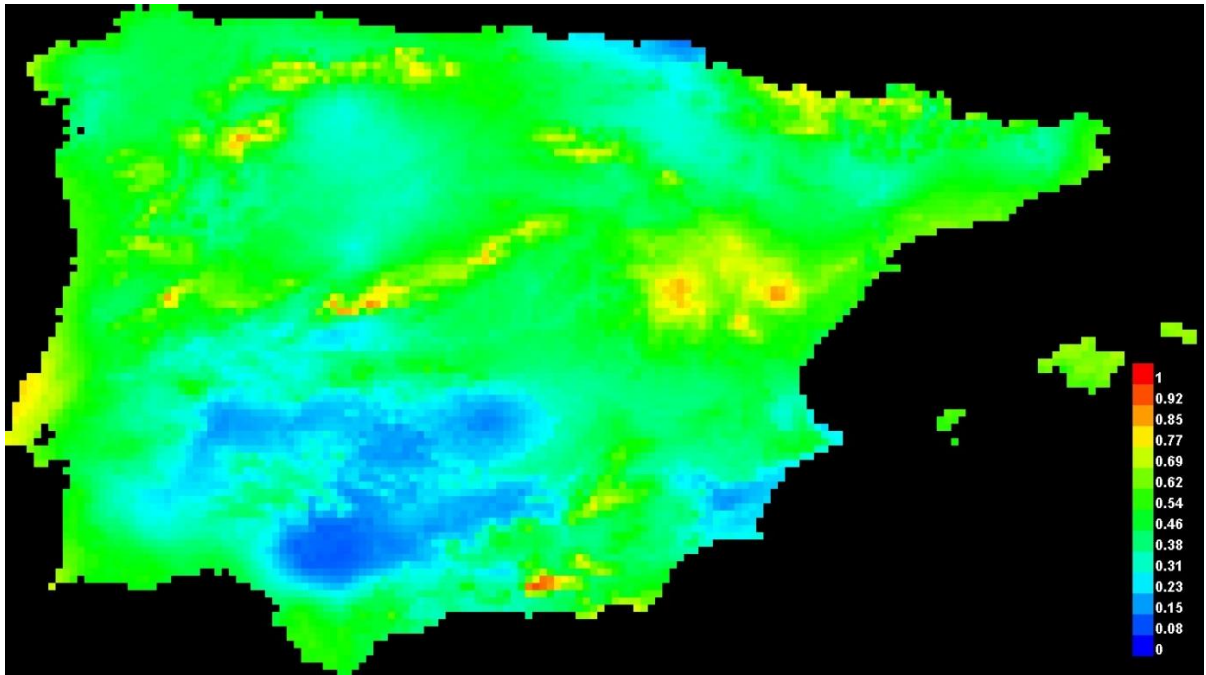
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711 SUPPLEMENTARY MATERIAL

712 **Appendix S1.** Individual SDM (logistic format) for each species following percentage of
713 prevalence order.

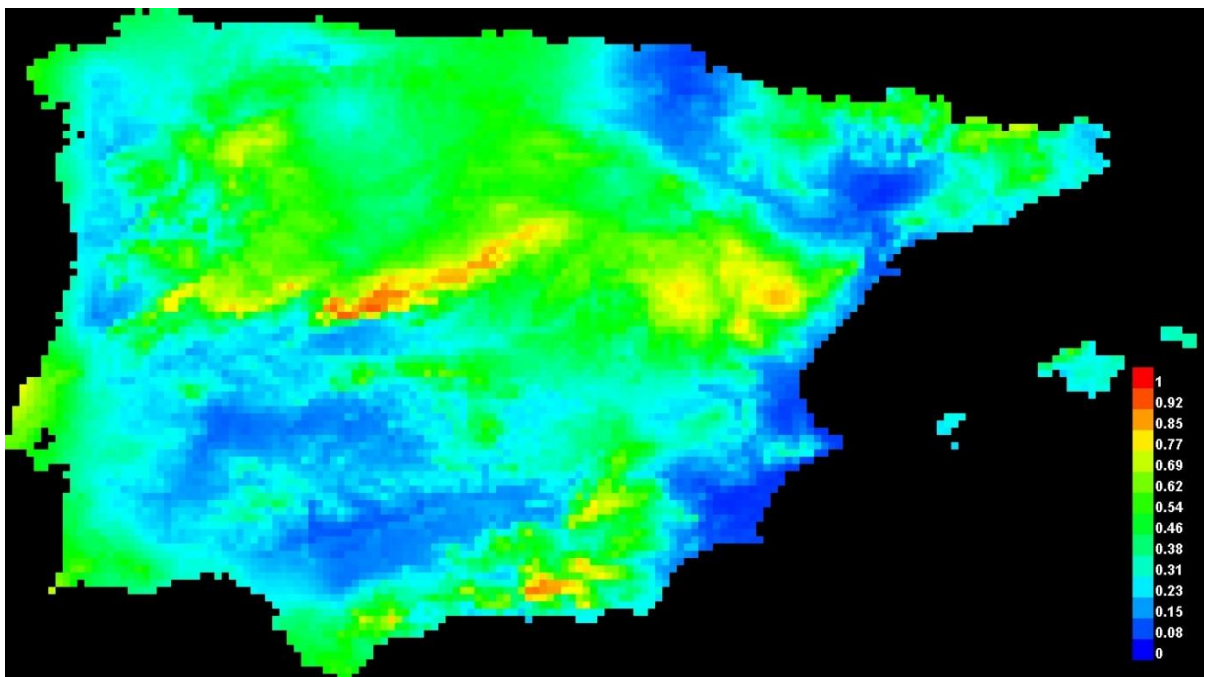
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715 Figure S1.1. *Bombus terrestris*



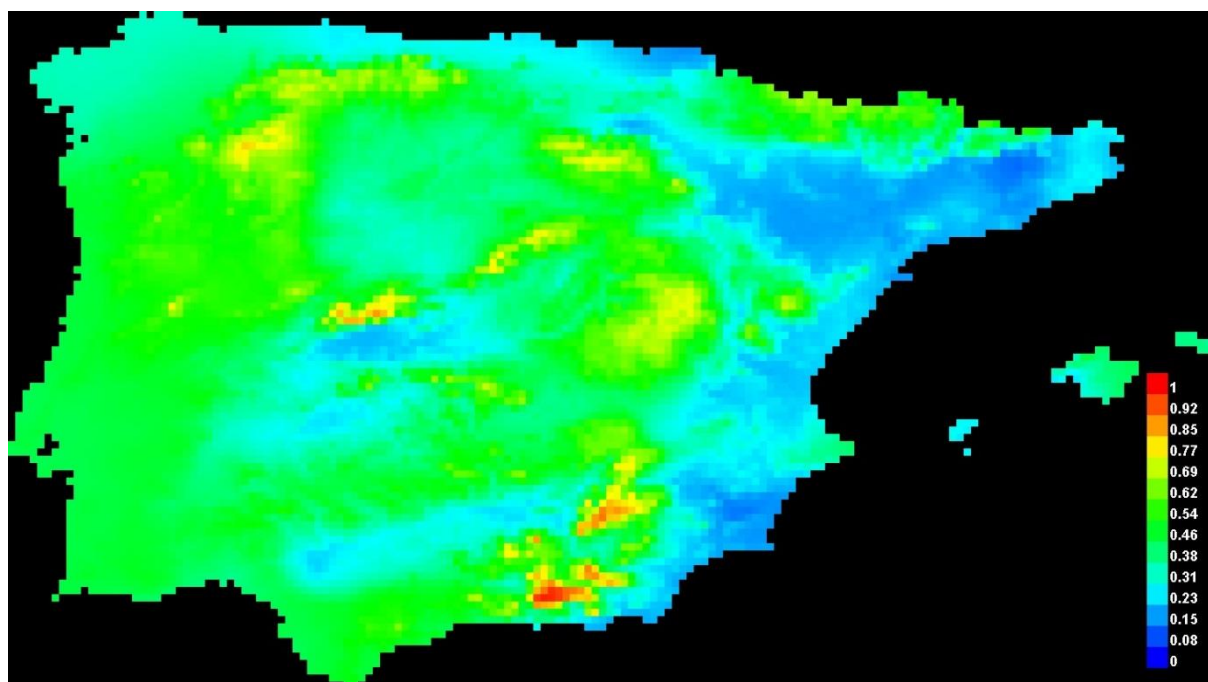
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717 Figure S1.2. *Bombus ruderatus*



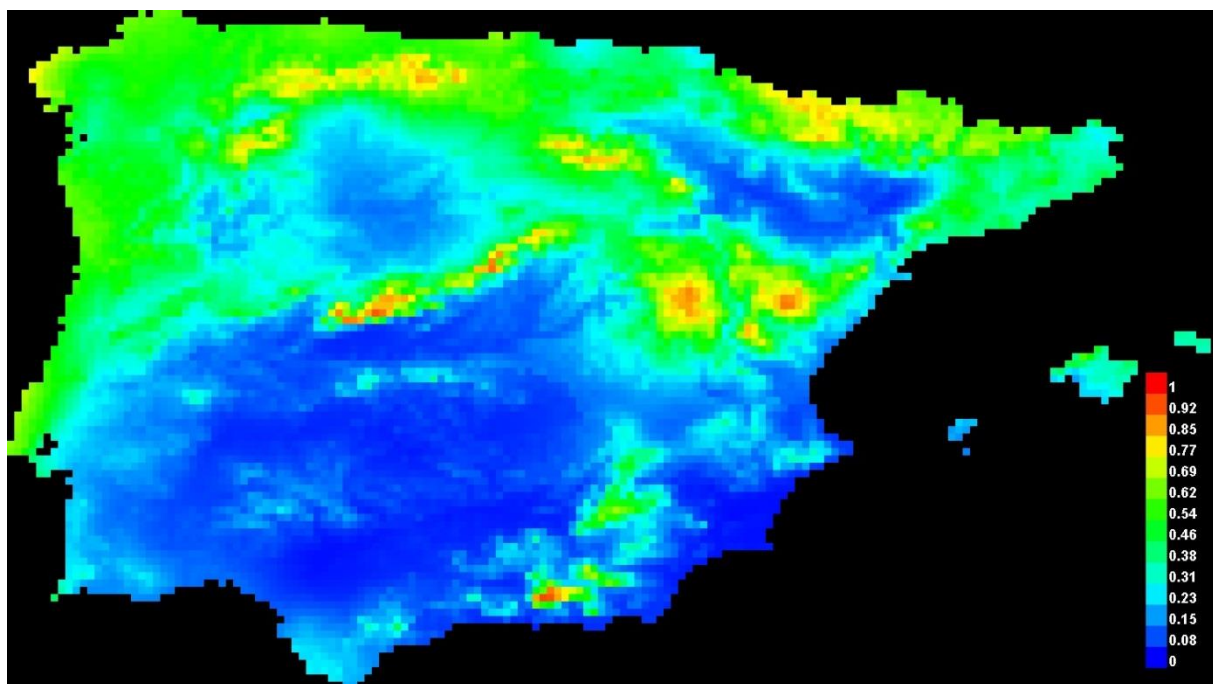
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719 Figure S1.3. *Bombus vestalis*



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721 Figure S1.4. *Bombus pascuorum*



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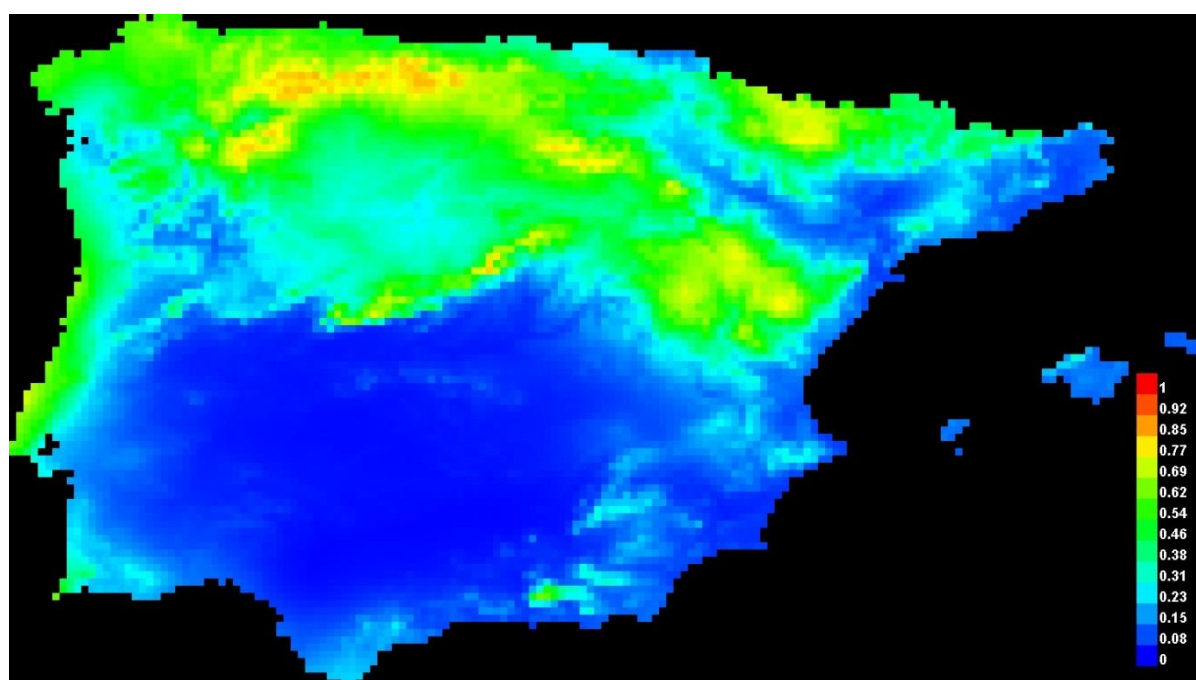
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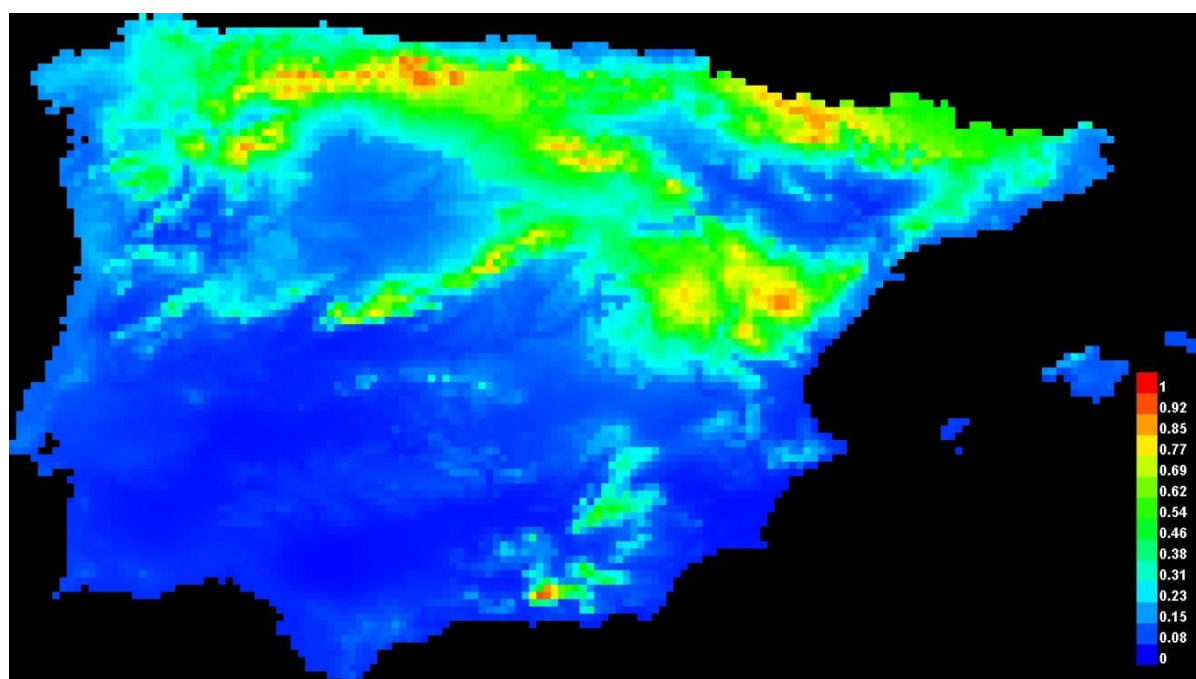
727 Figure S1.5. *Bombus muscorum*



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730 Figure S1.6. *Bombus pratorum*



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Figure S1.7. *Bombus hortorum*

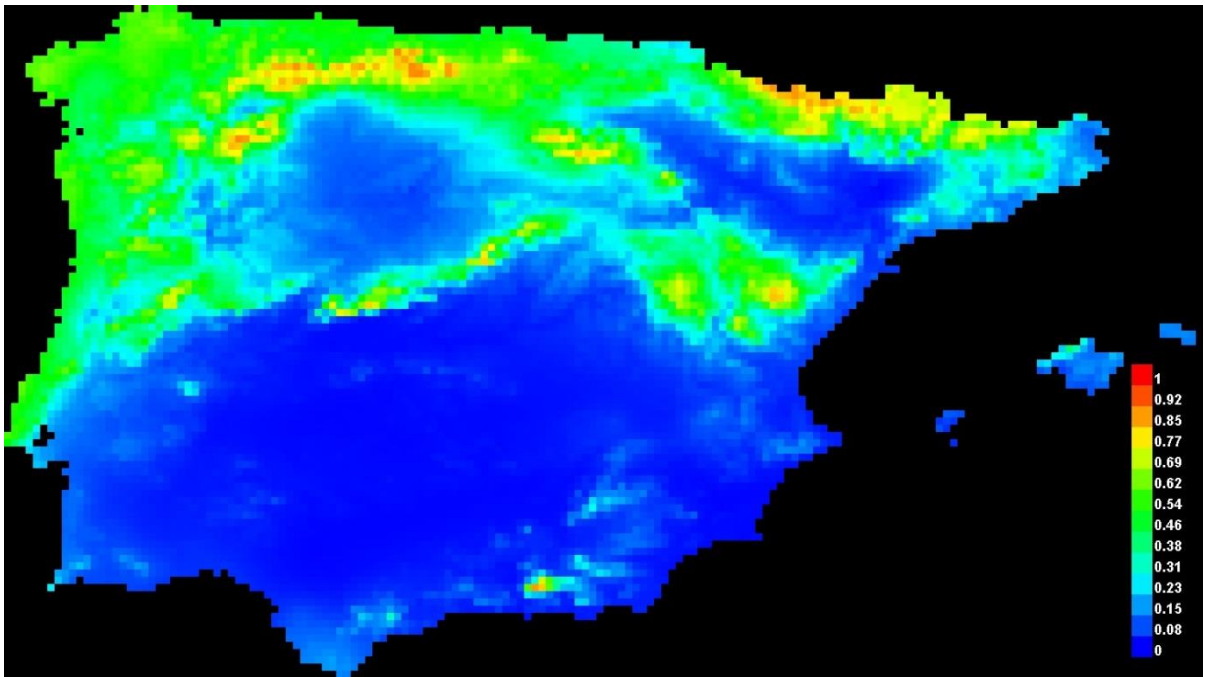
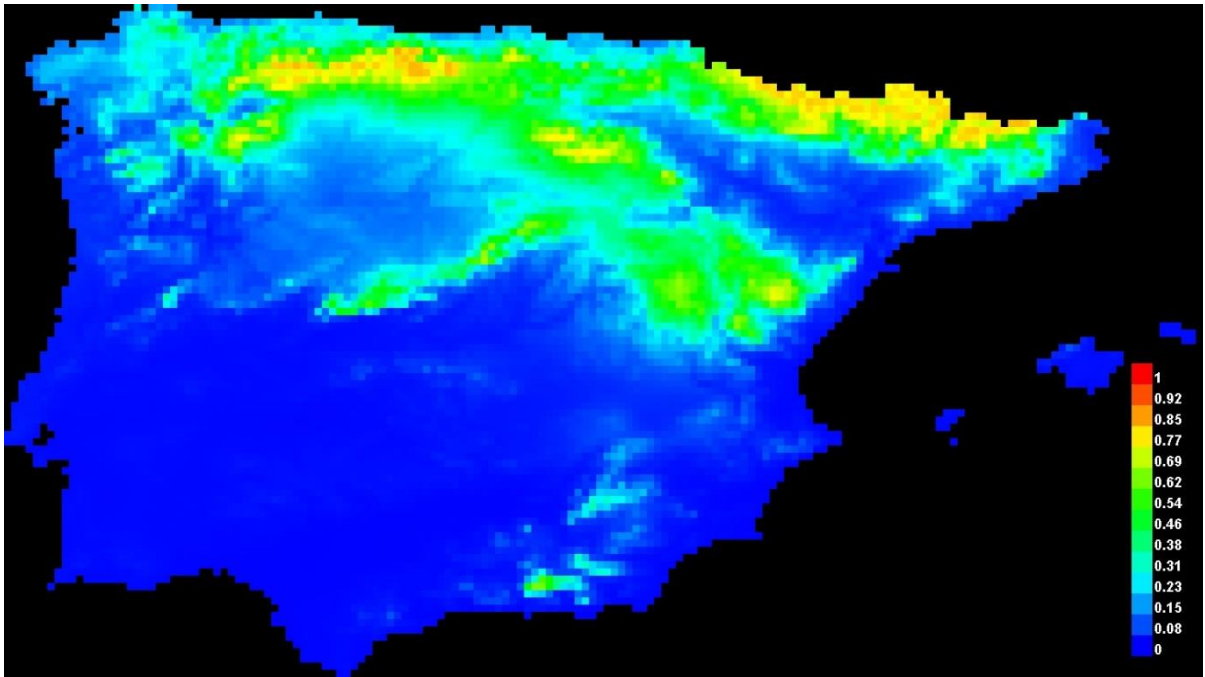
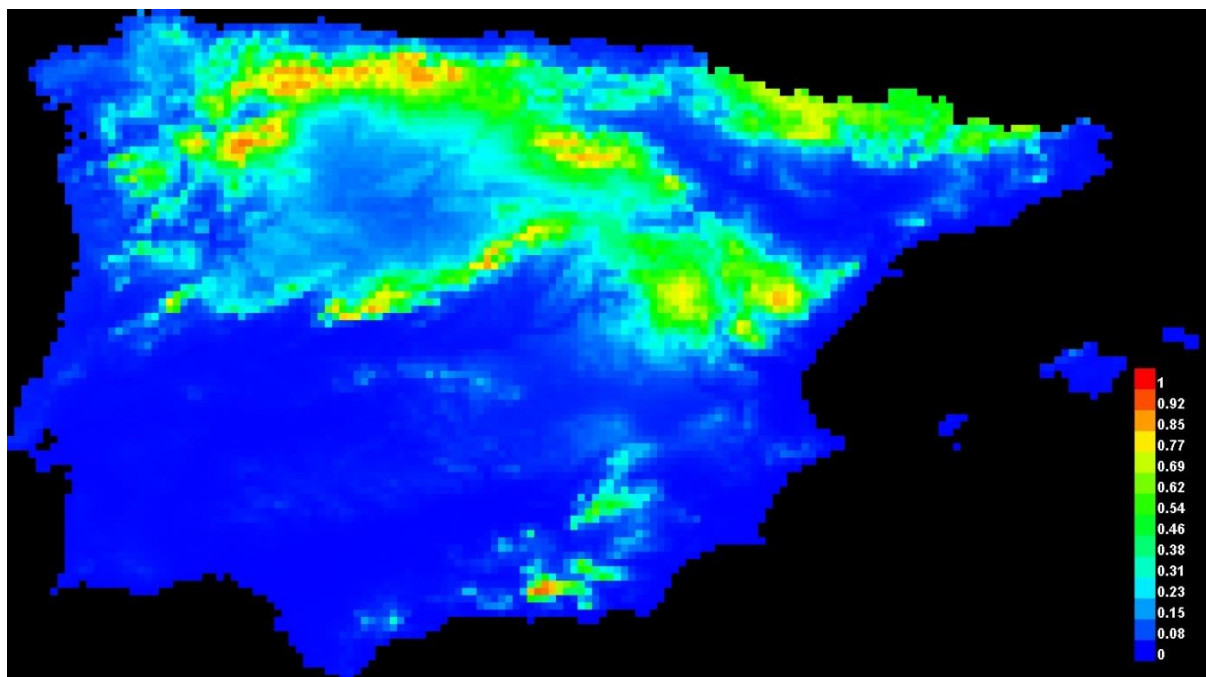


Figure S1.8. *Bombus cullumanus*



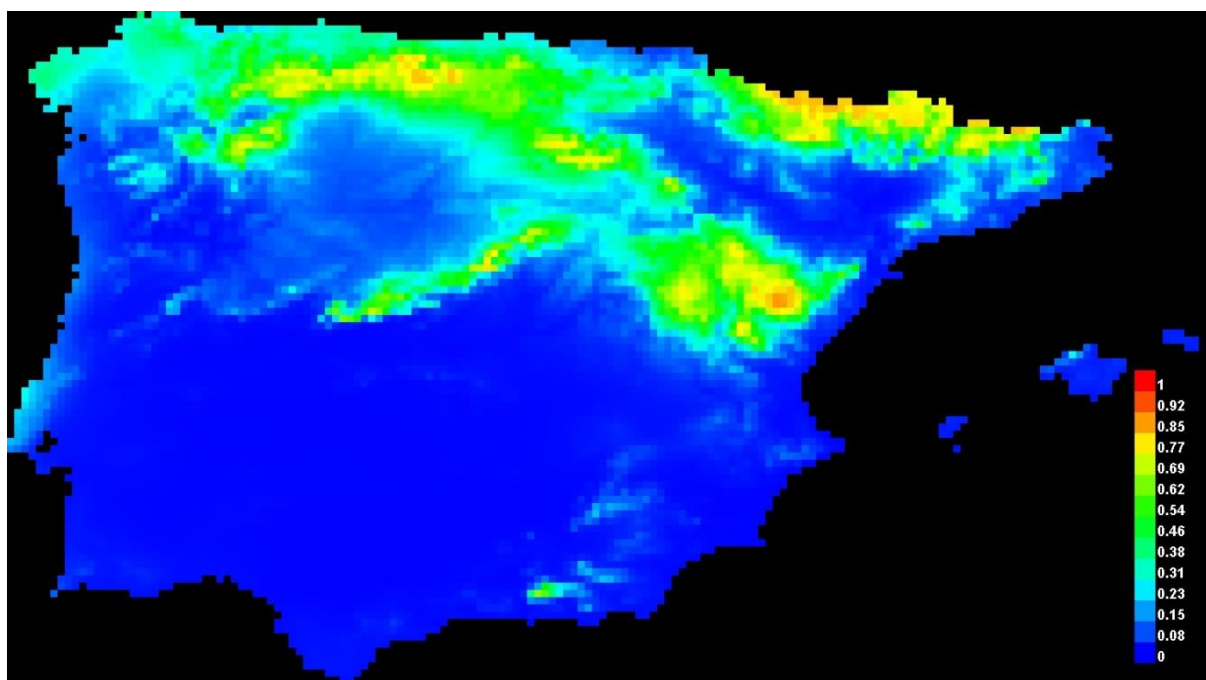
749 Figure S1.9. *Bombus barbutellus*



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752 Figure S1.10. *Bombus humilis*



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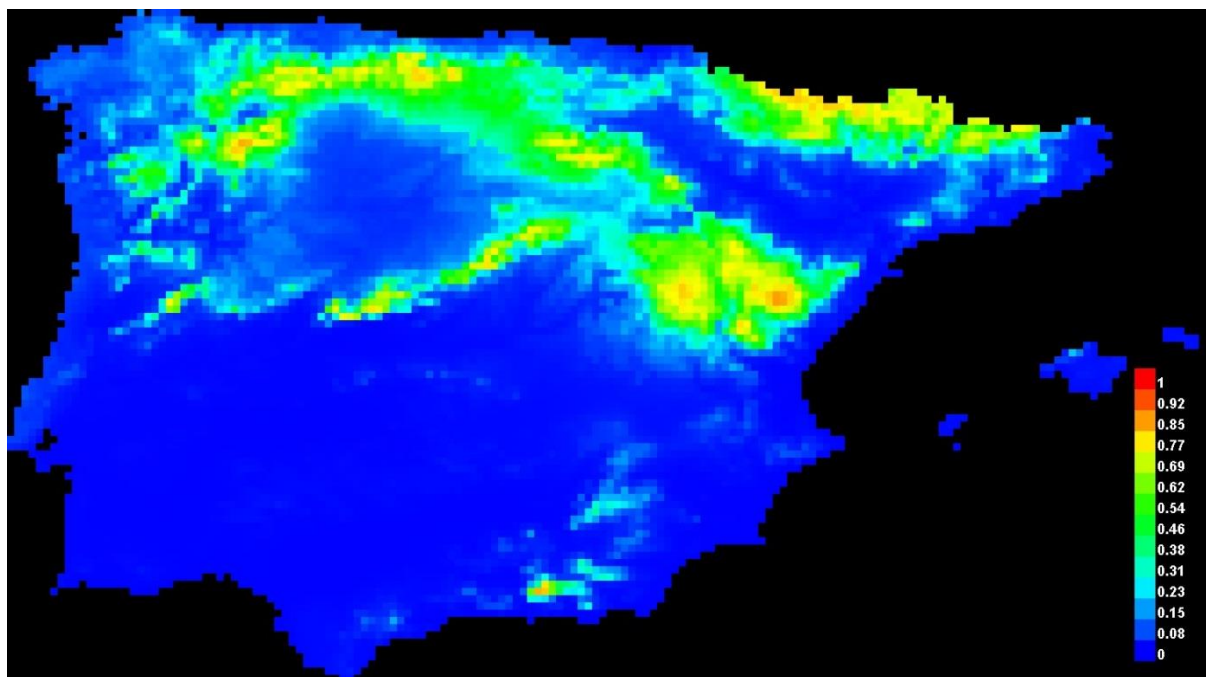
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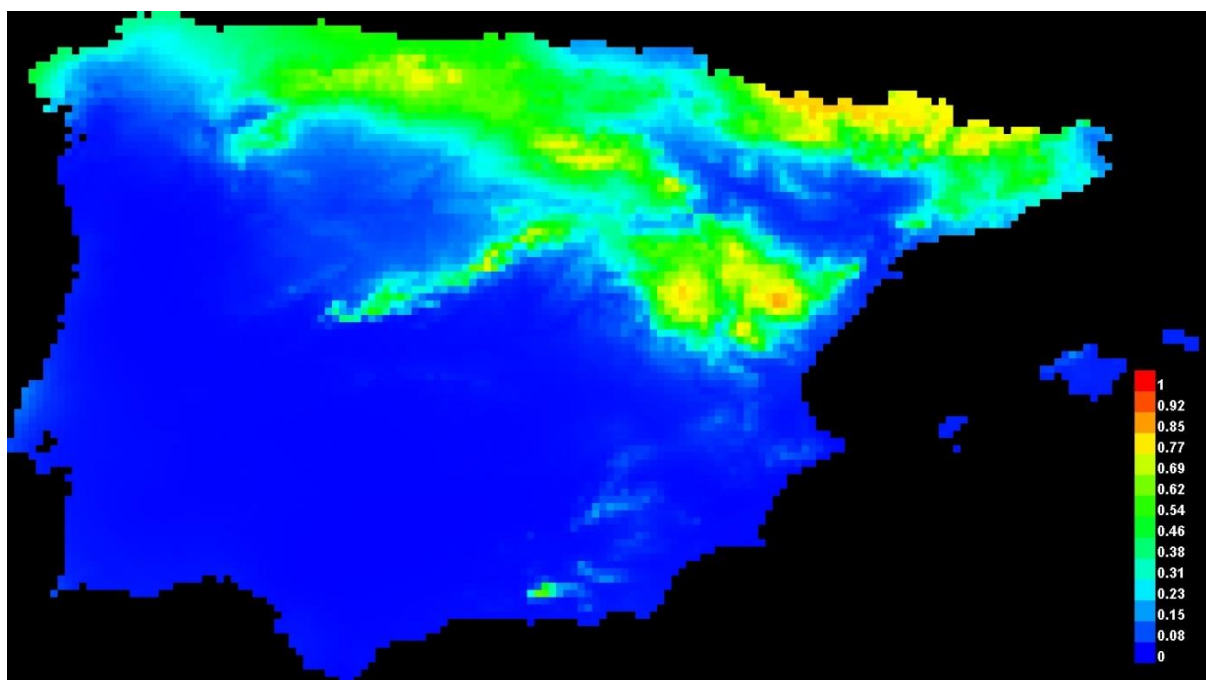
760 Figure S1.11. *Bombus lapidarius*



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763 Figure S1.12. *Bombus sylvarum*



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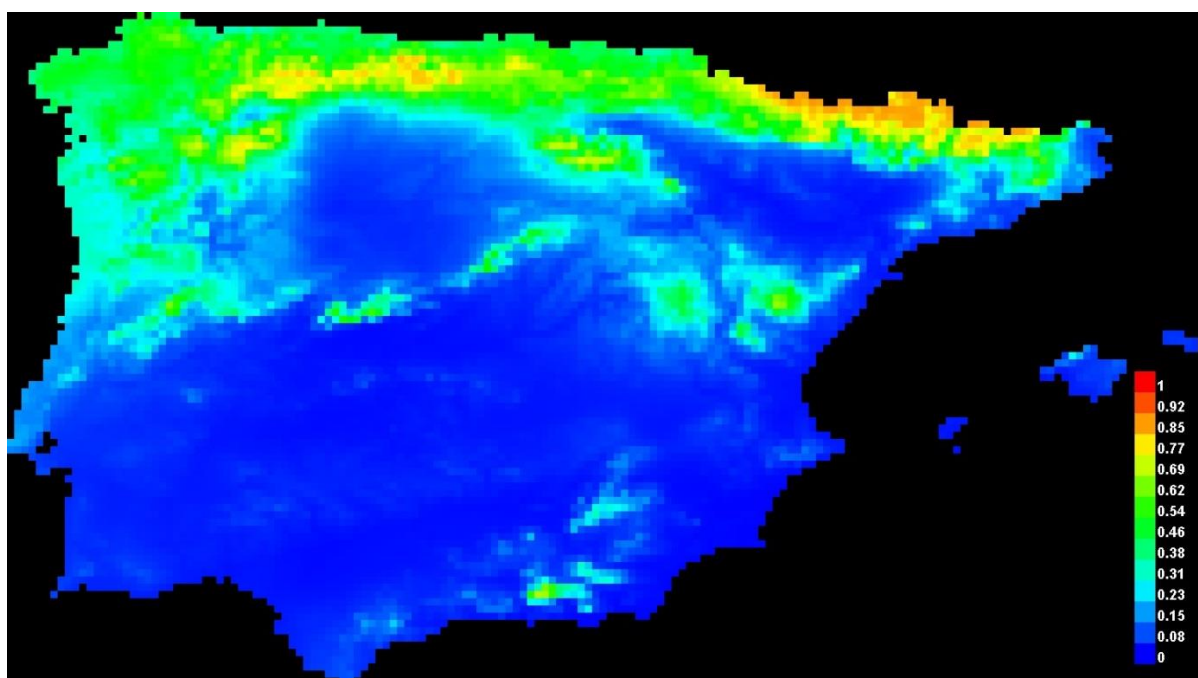
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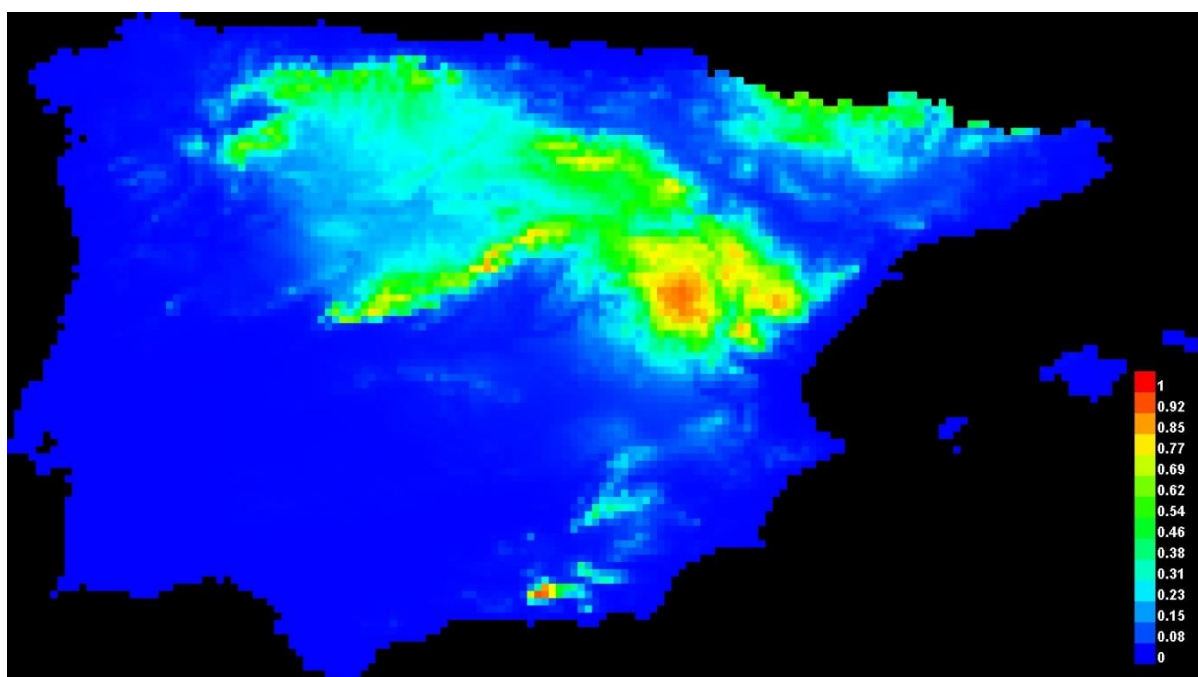
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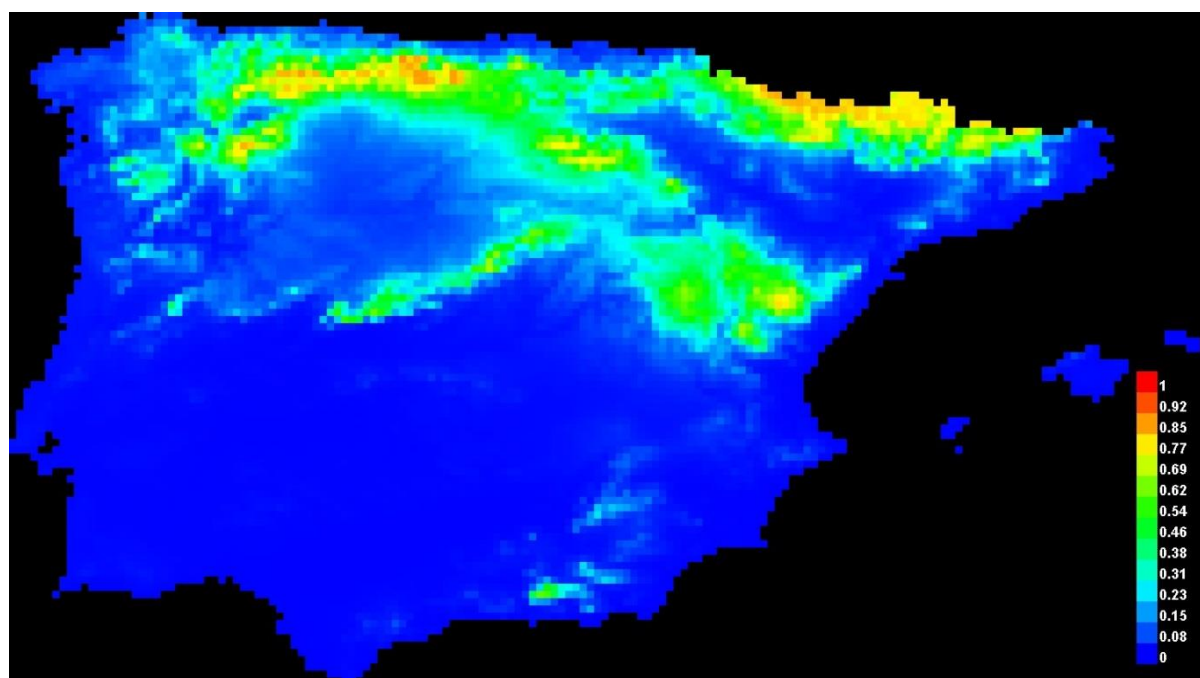
771 Figure S1.13. *Bombus campestris*



775 Figure S1.14. *Bombus mocsaryi*



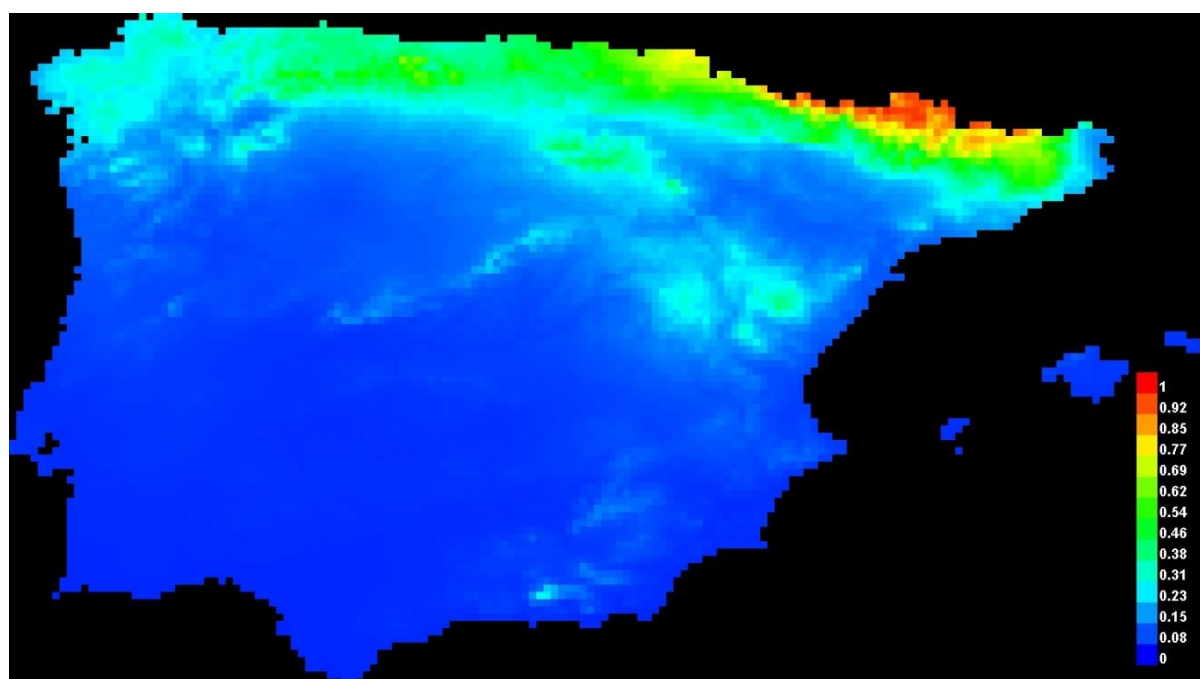
782 Figure S1.15. *Bombus sylvestris*



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785 Figure S1.16. *Bombus confusus*



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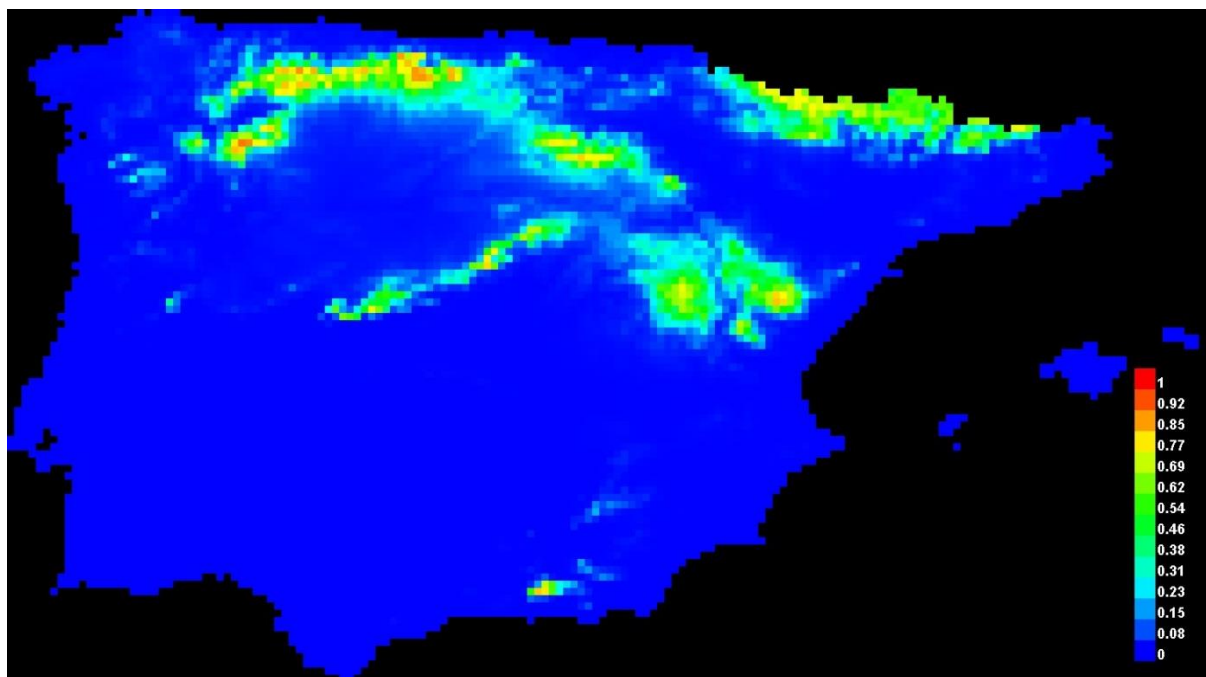
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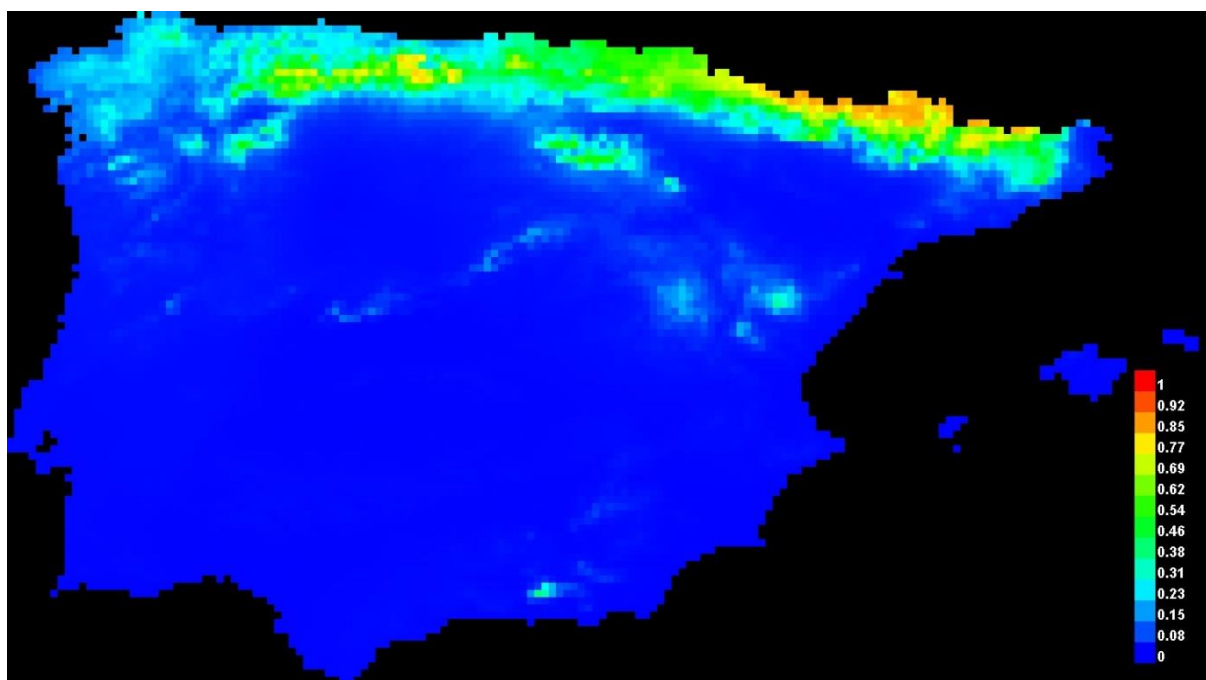
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793 Figure S1.17. *Bombus rupestris*

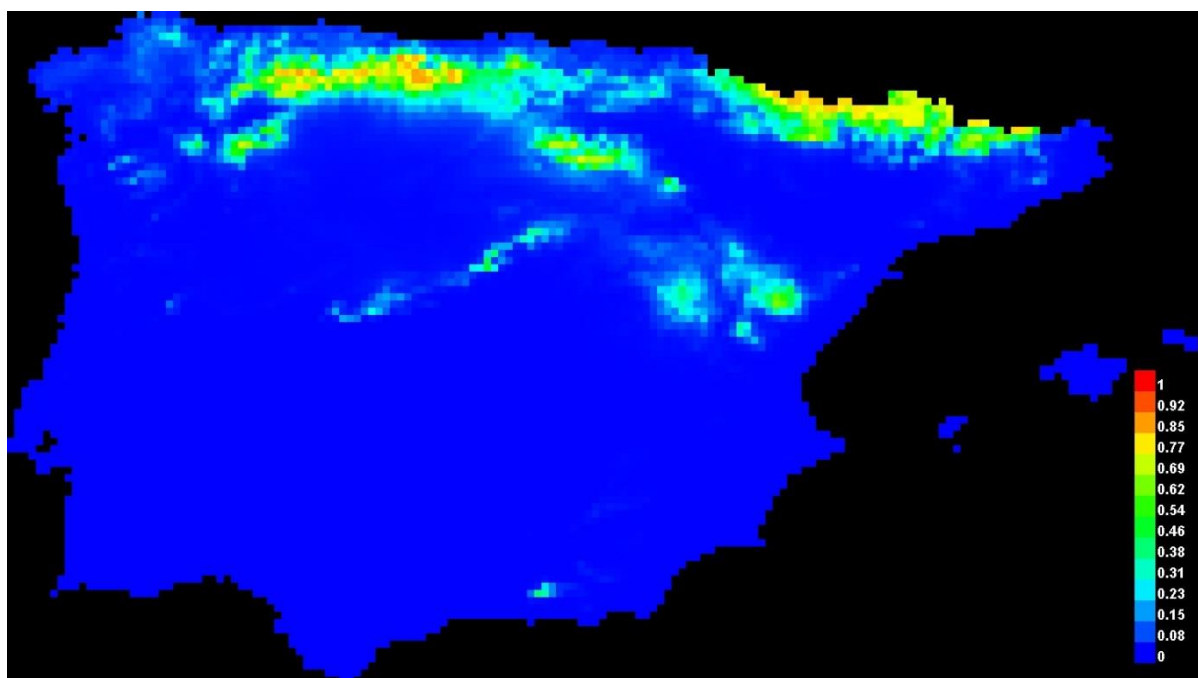


796 Figure S1.18. *Bombus hypnorum*



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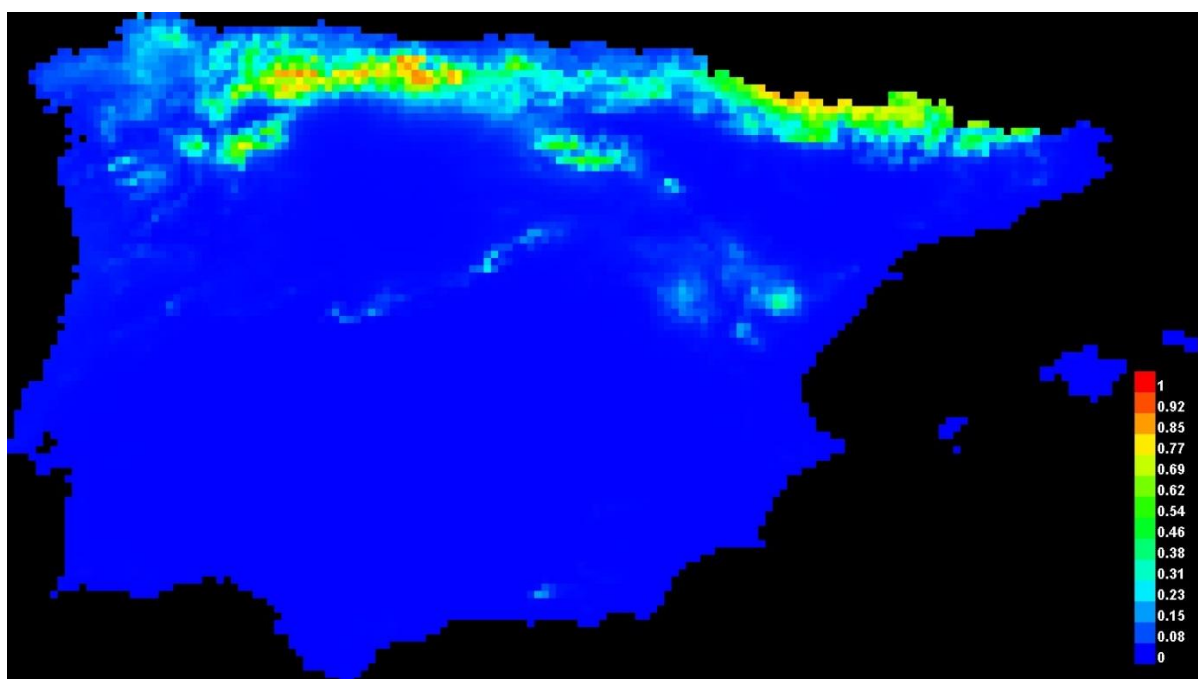
805 Figure S1.19. *Bombus ruderarius*



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808 Figure S1.20. *Bombus wurflenii*



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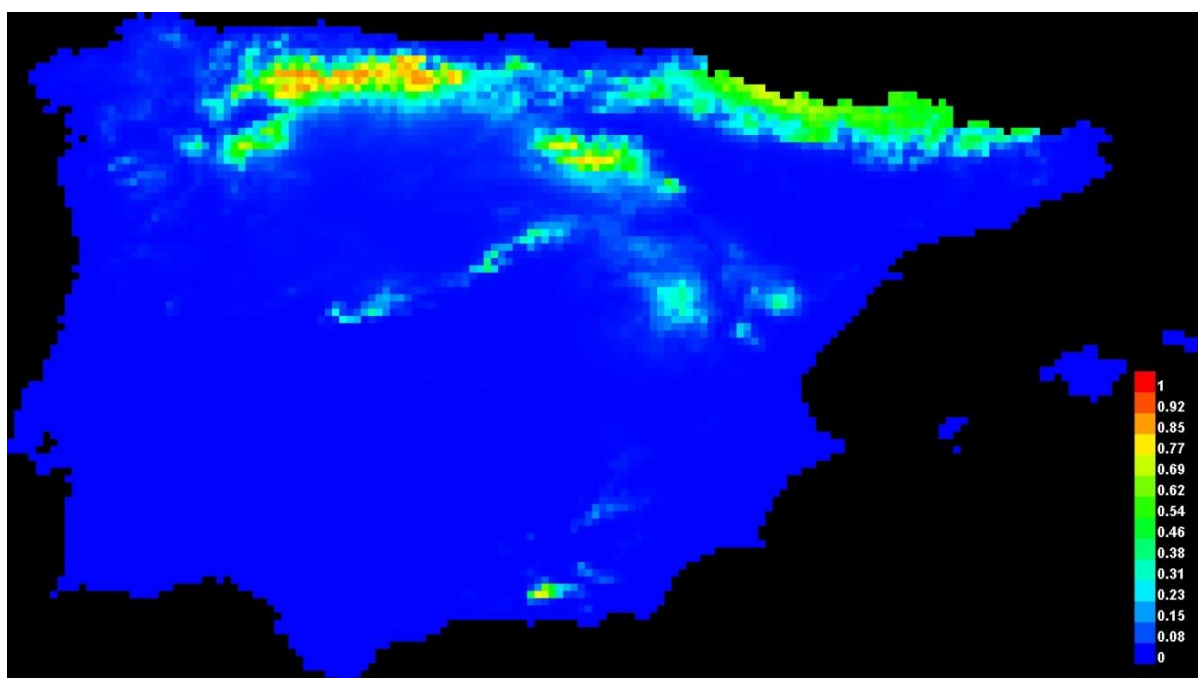
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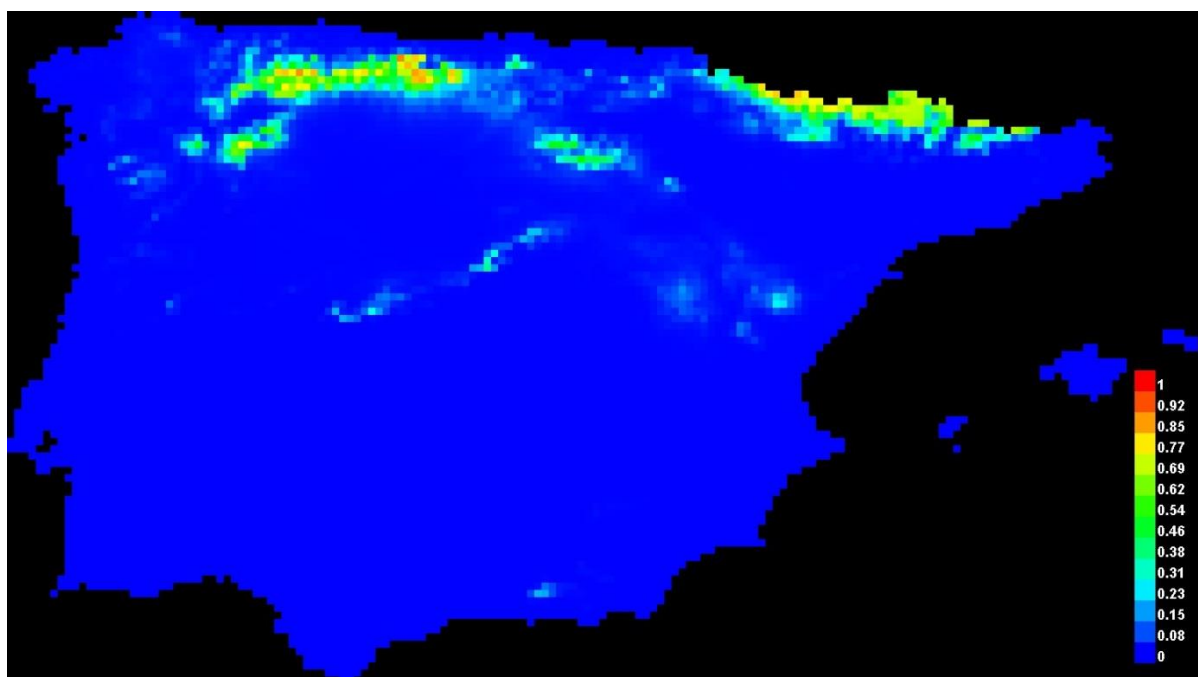
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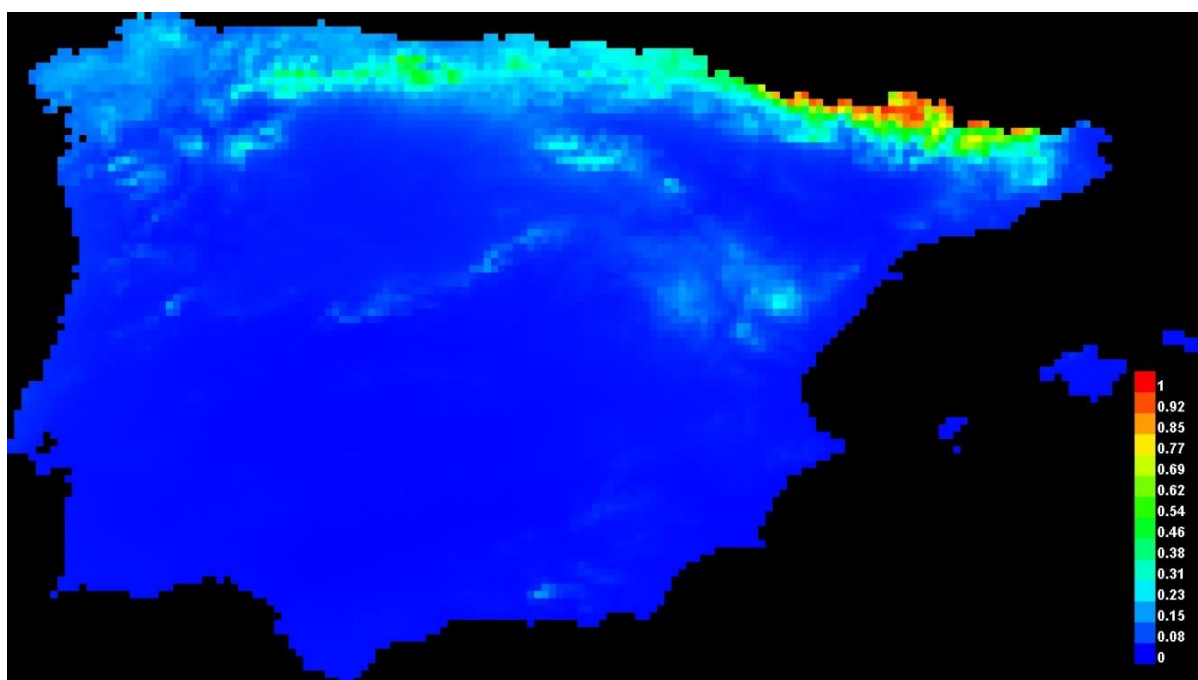
815 Figure S1.21. *Bombus jonellus*



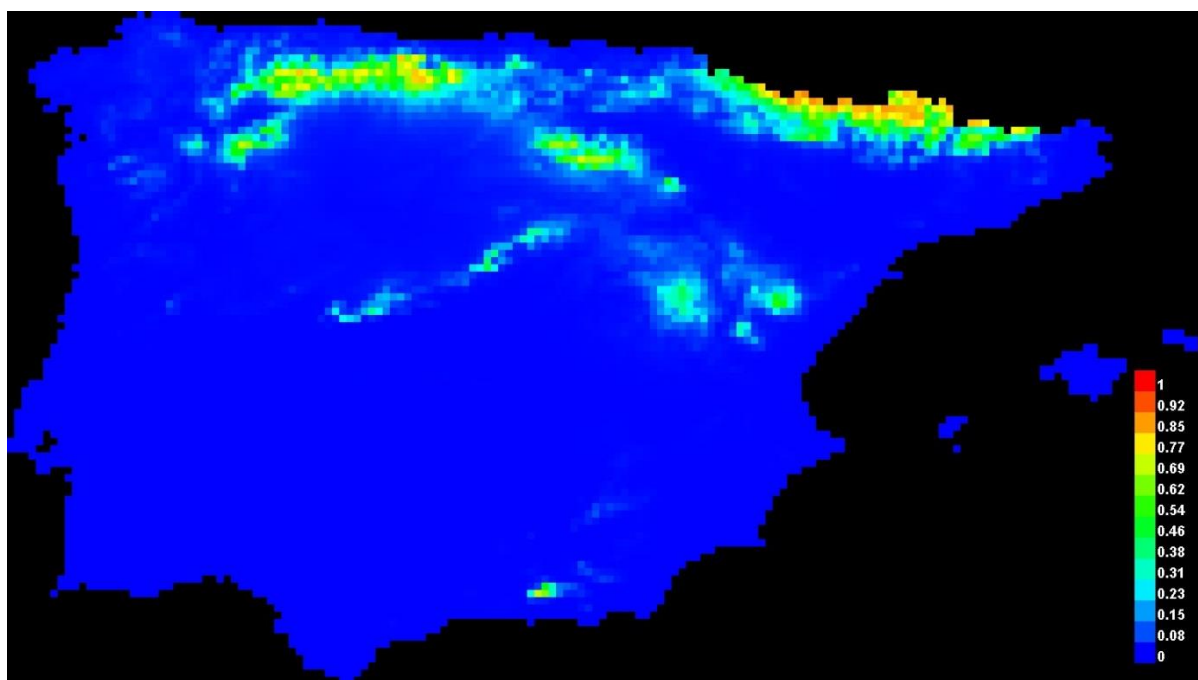
818 Figure S1.22. *Bombus mesomelas*



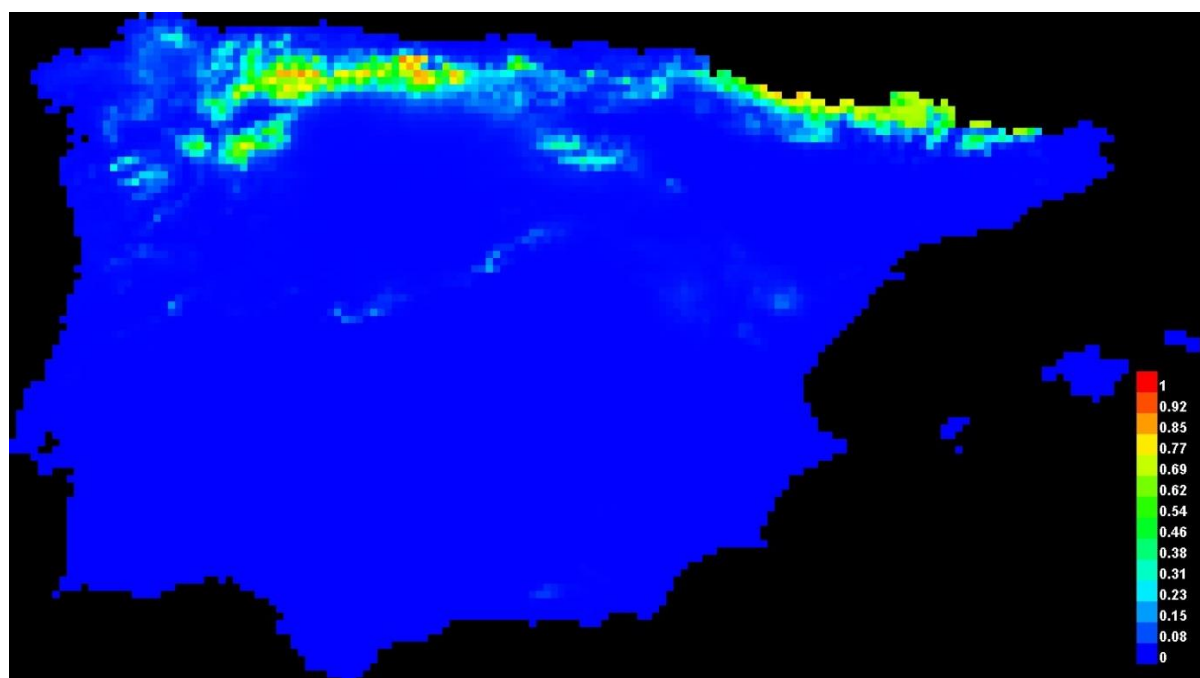
826 Figure S1.23. *Bombus mendax*



829 Figure S1.24. *Bombus bohemicus*



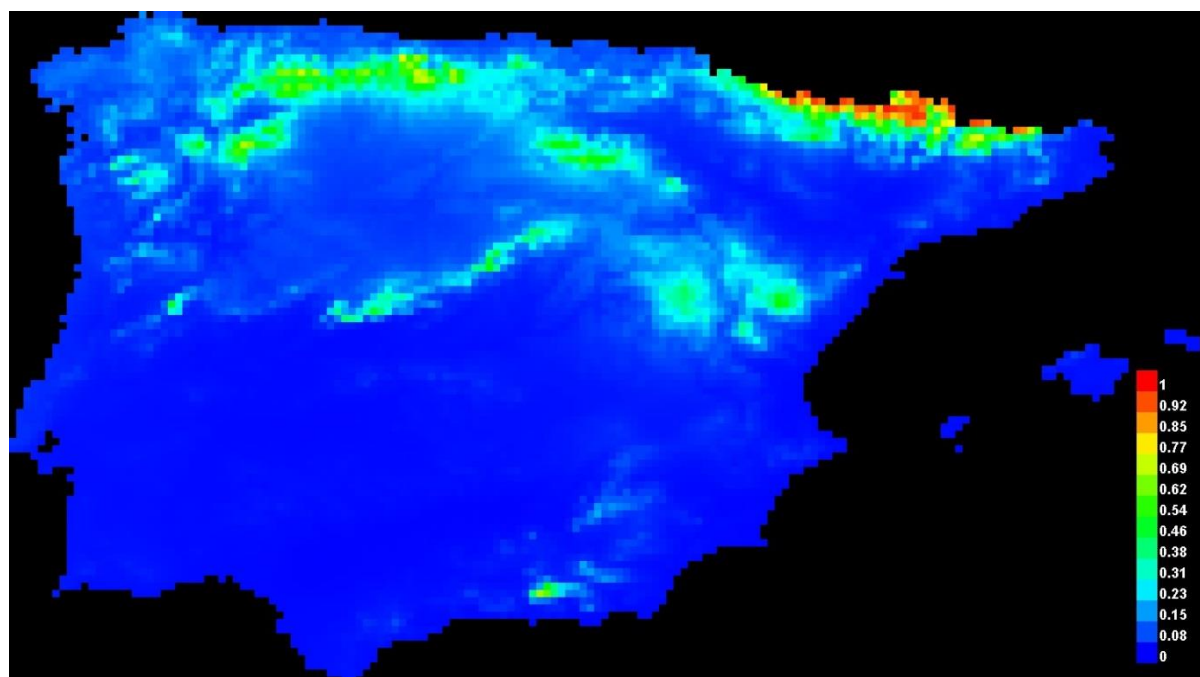
837 Figure S1.25. *Bombus soroeensis*



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840 Figure S1.26. *Bombus quadricolor*



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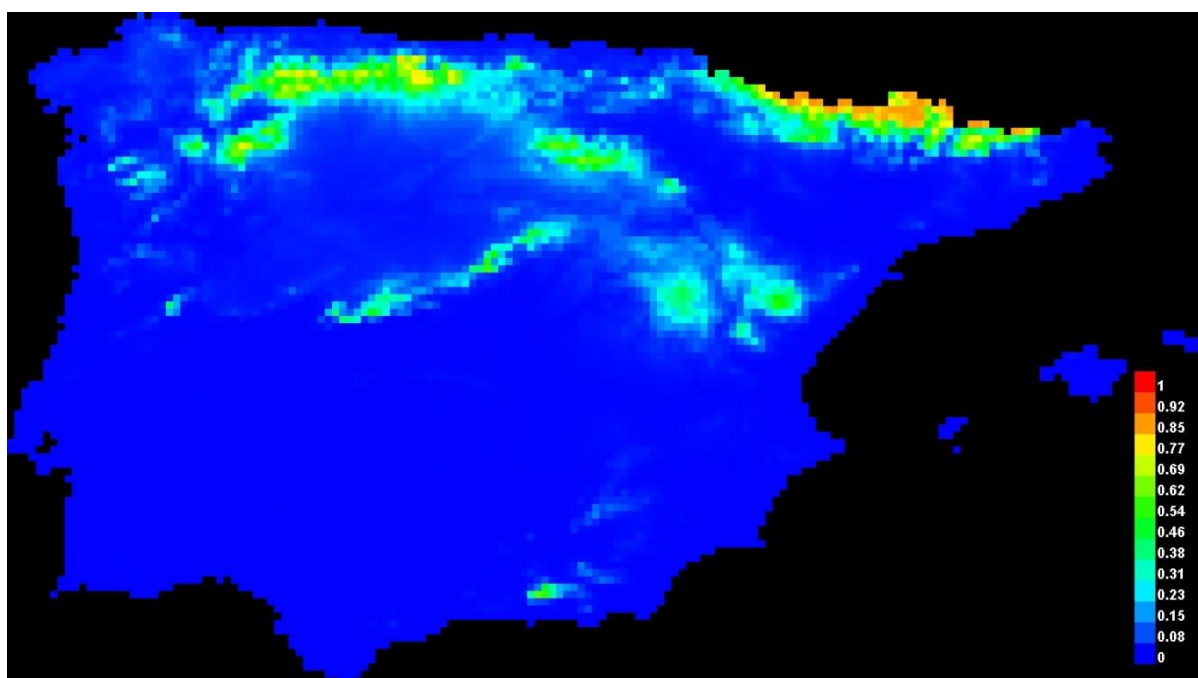
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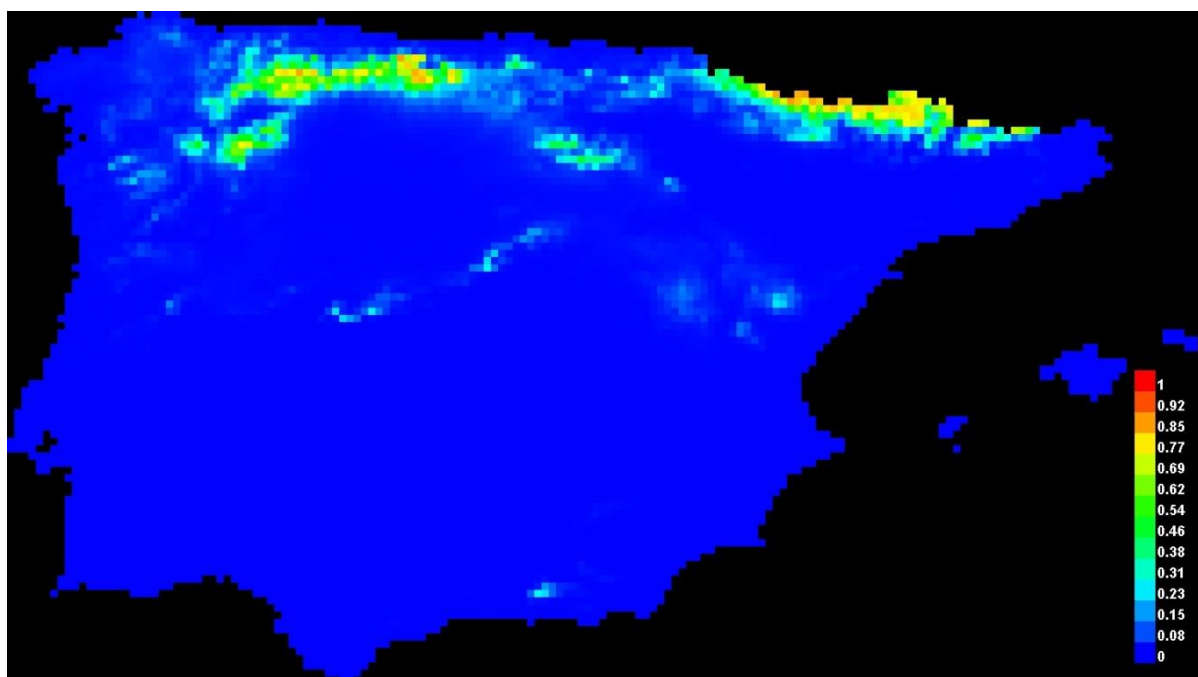
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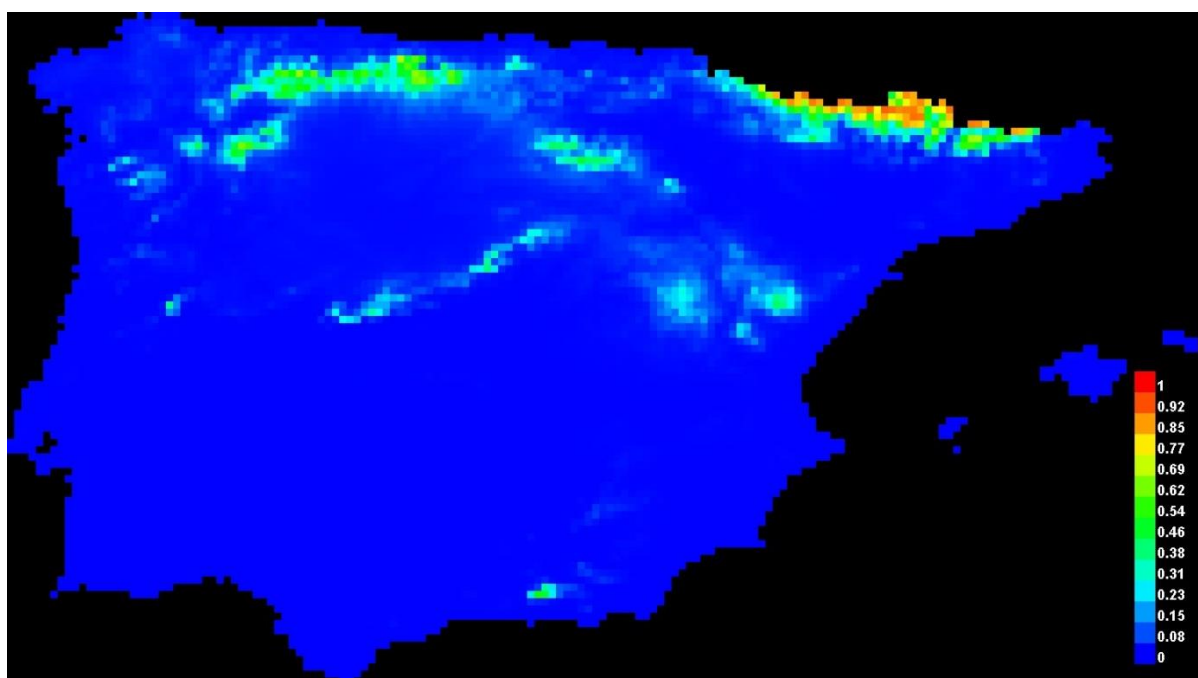
848 Figure S1.27. *Bombus subterraneus*



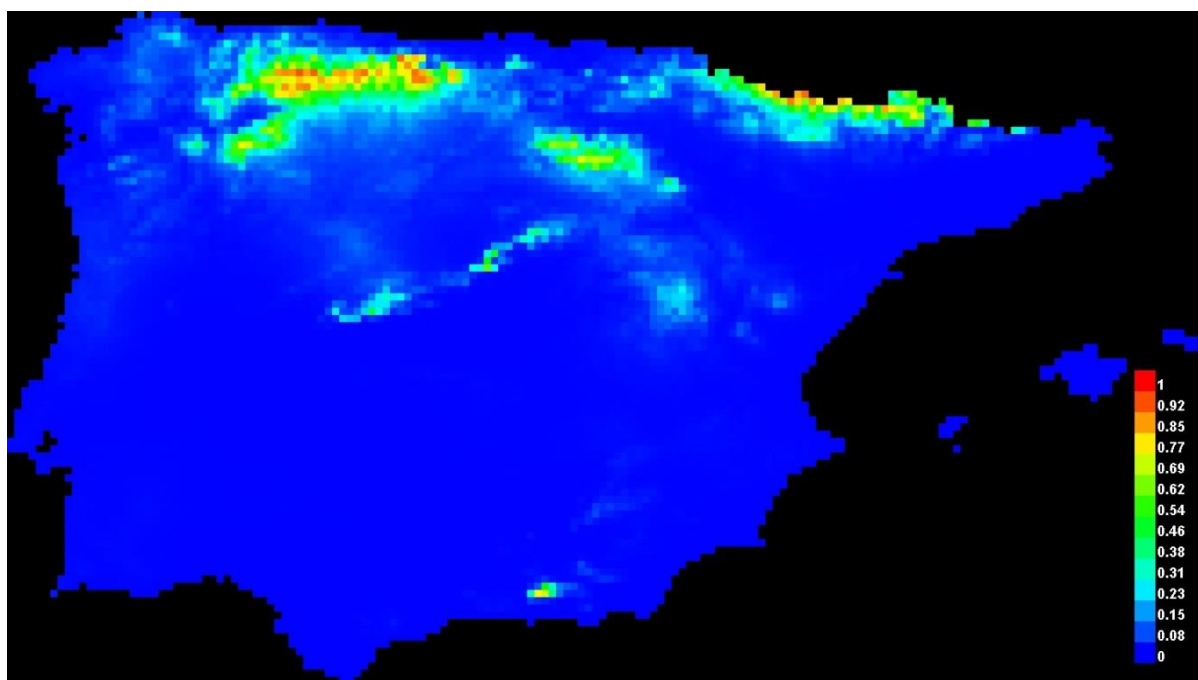
851 Figure S1.28. *Bombus sichelii*



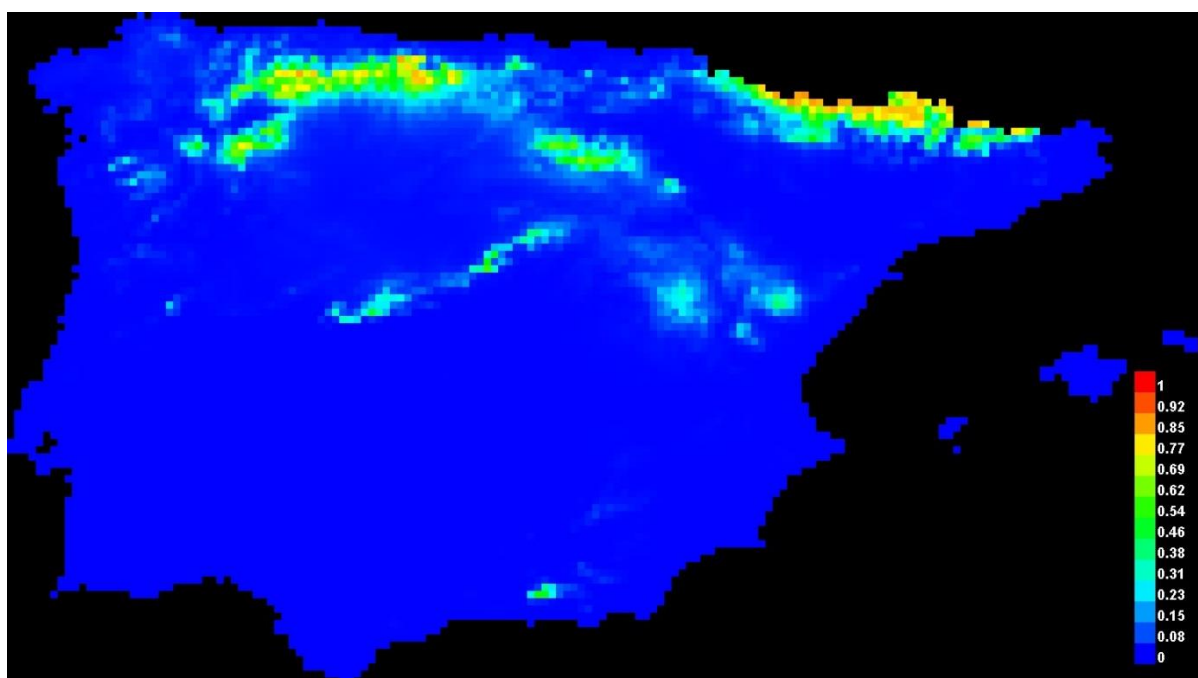
859 Figure S1.29. *Bombus monticola*



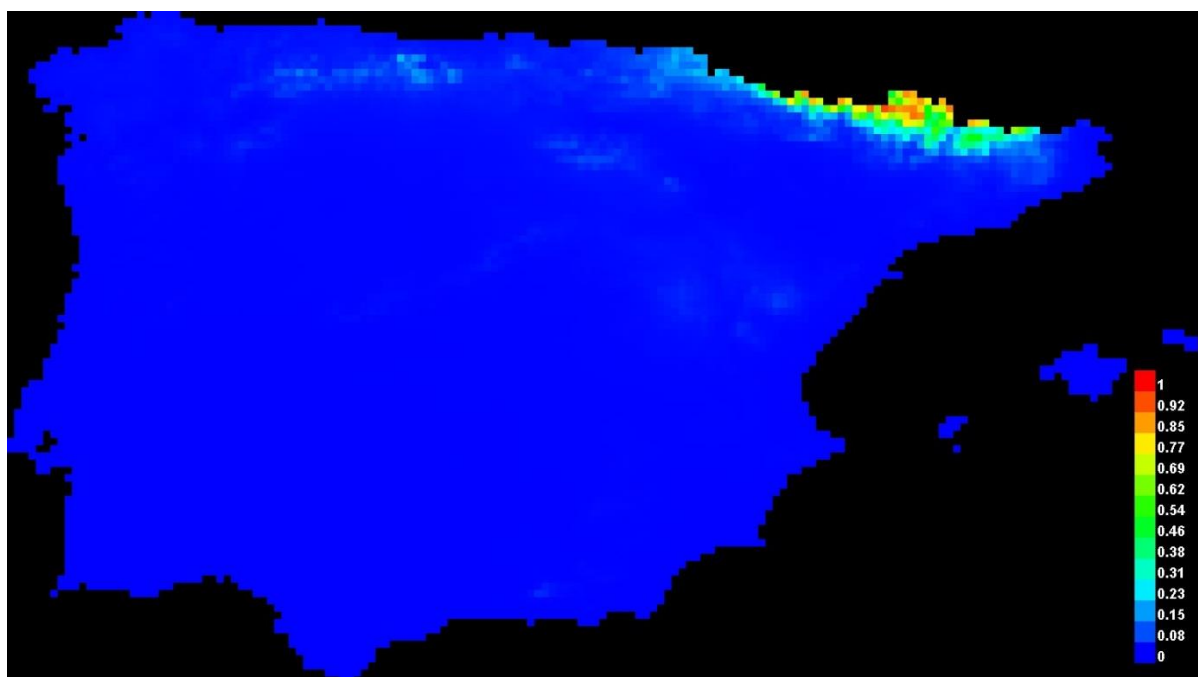
862 Figure S1.30. *Bombus inexpectatus*



870 Figure S1.31. *Bombus mucedus*



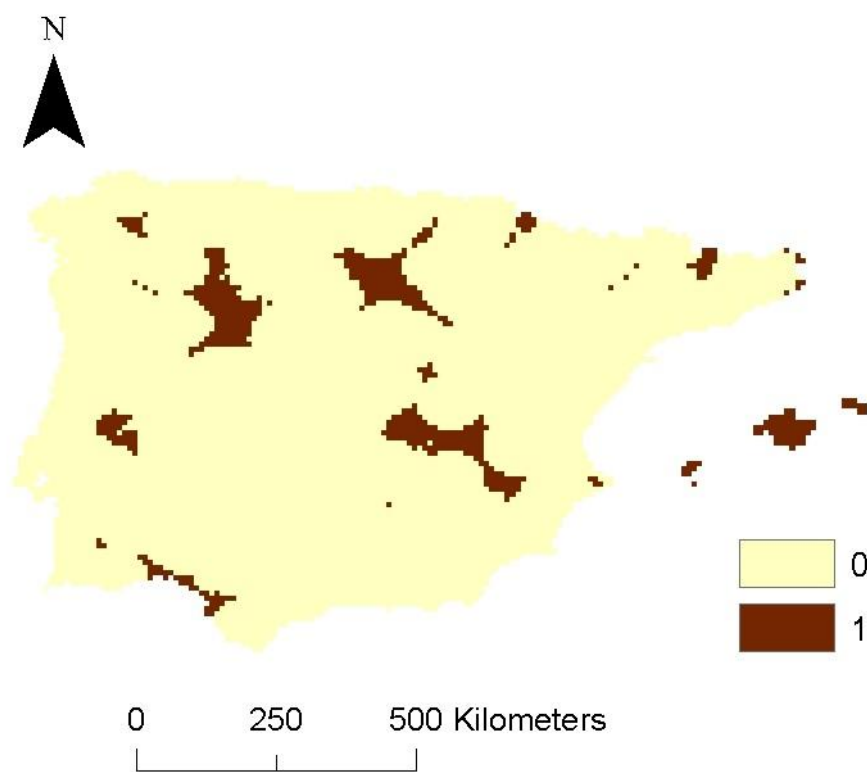
873 Figure S1.32. *Bombus pyrenaicus*



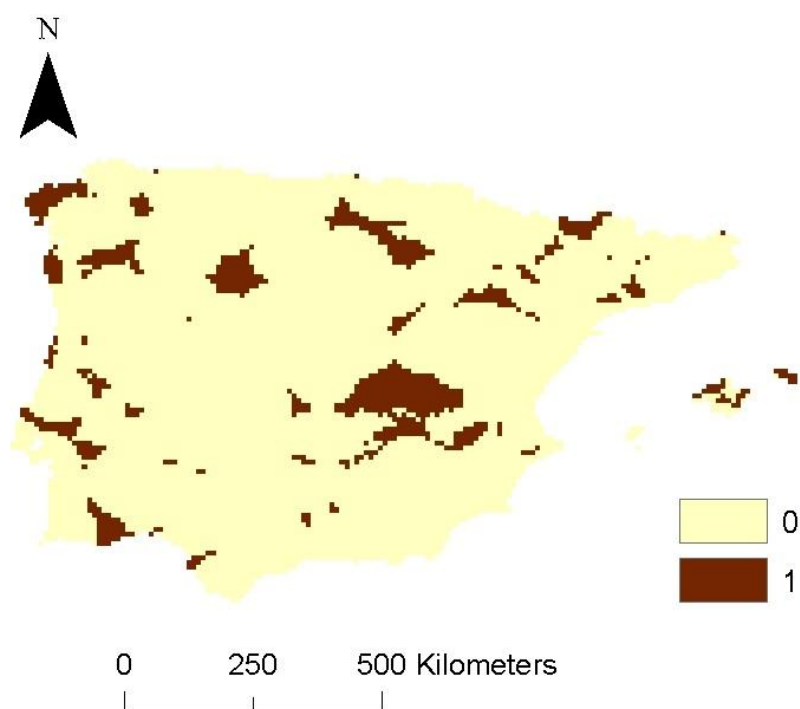
881 **Appendix S2.** Undersampled area for each species (1-undersampled, 0- not undersampled).

882

883 Figure S2.1. *Bombus terrestris*

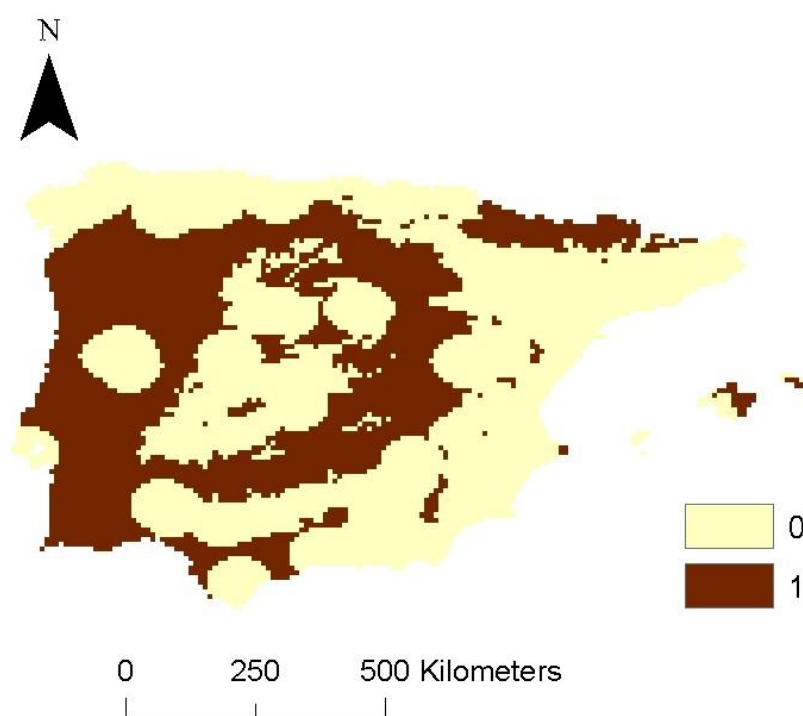


894 Figure S2.2. *Bombus ruderatus*



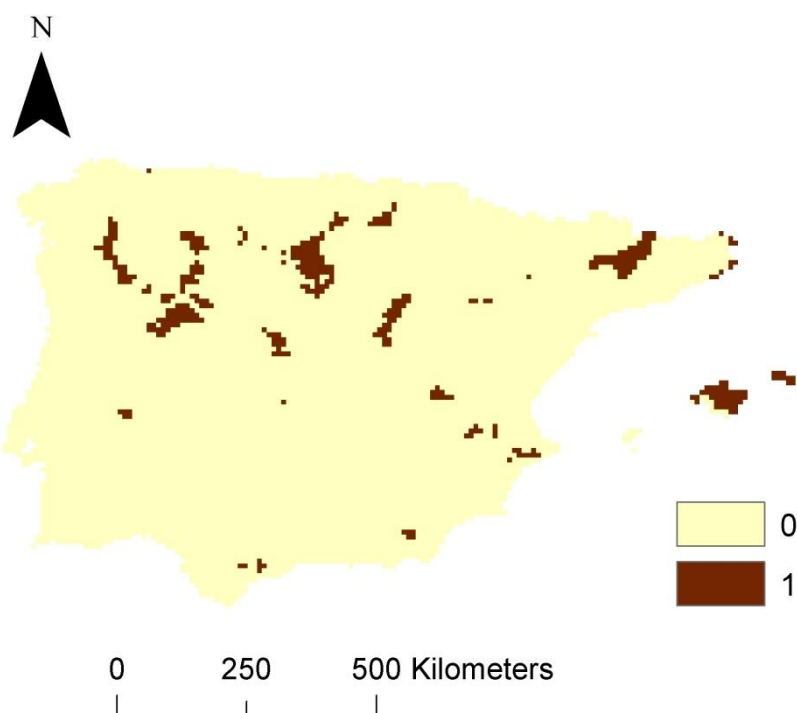
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896 Figure S2.3. *Bombus vestalis*



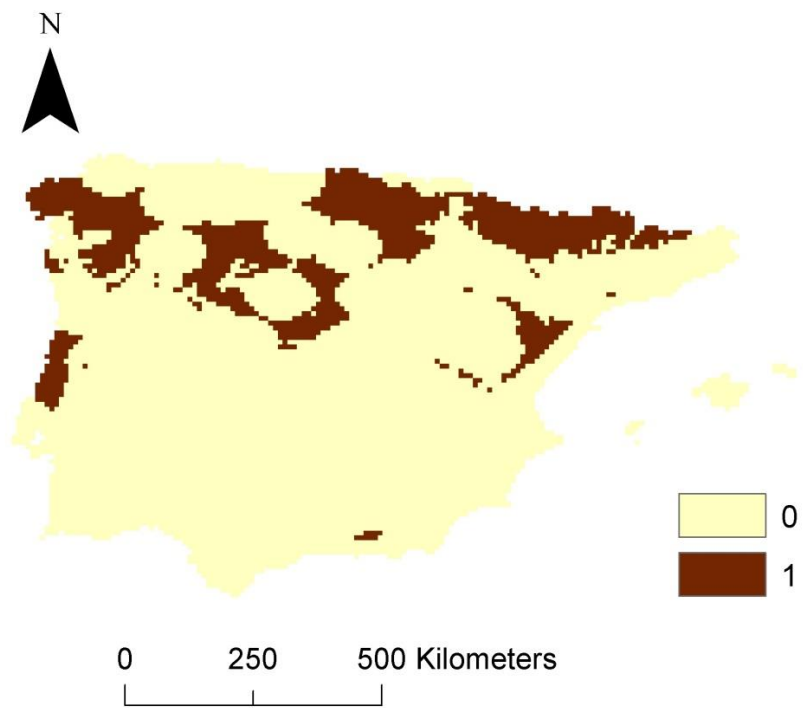
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907 Figure S2.4. *Bombus pascuorum*



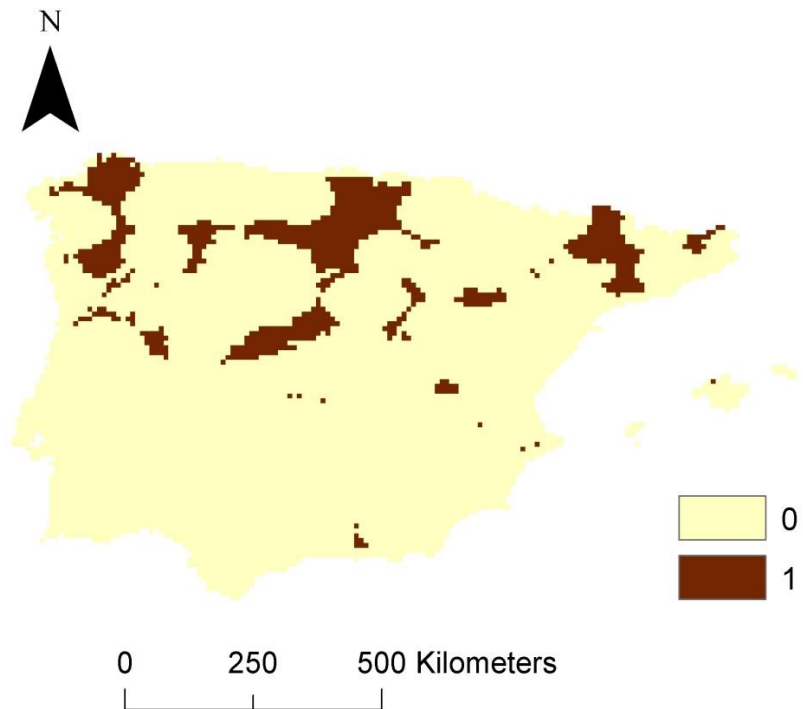
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919 Figure S2.5. *Bombus muscorum*



920

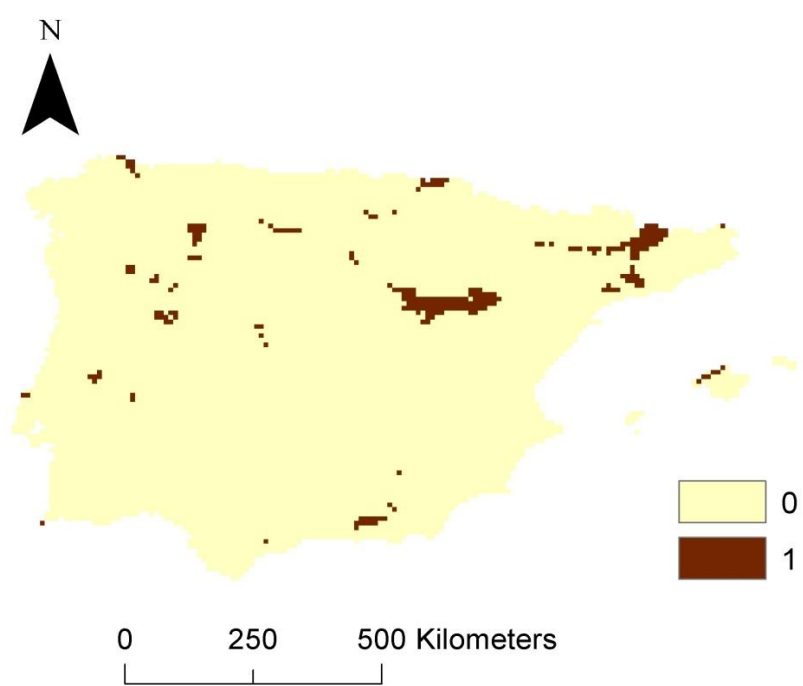
921 Figure S2.6. *Bombus pratorum*



922

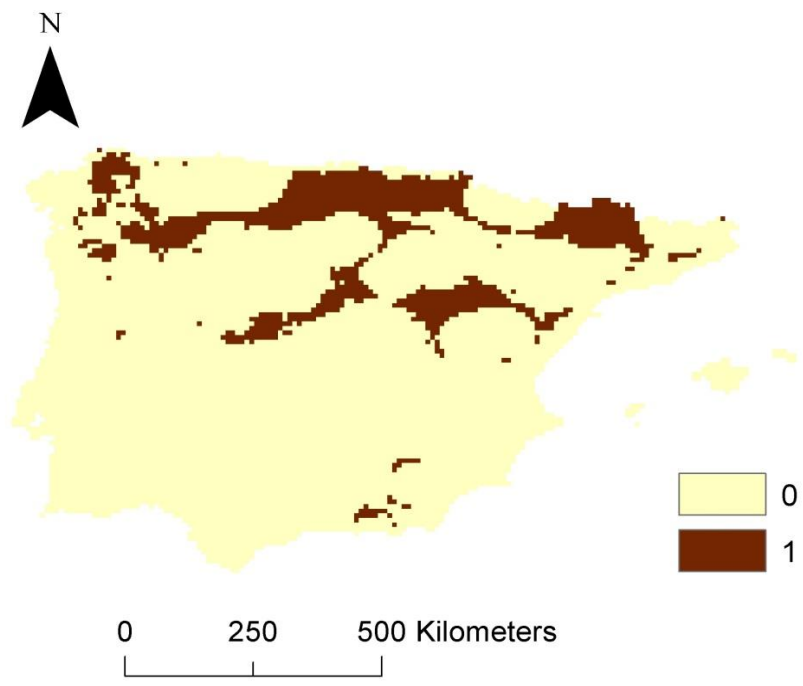
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924 Figure S2.7. *Bombus hortorum*



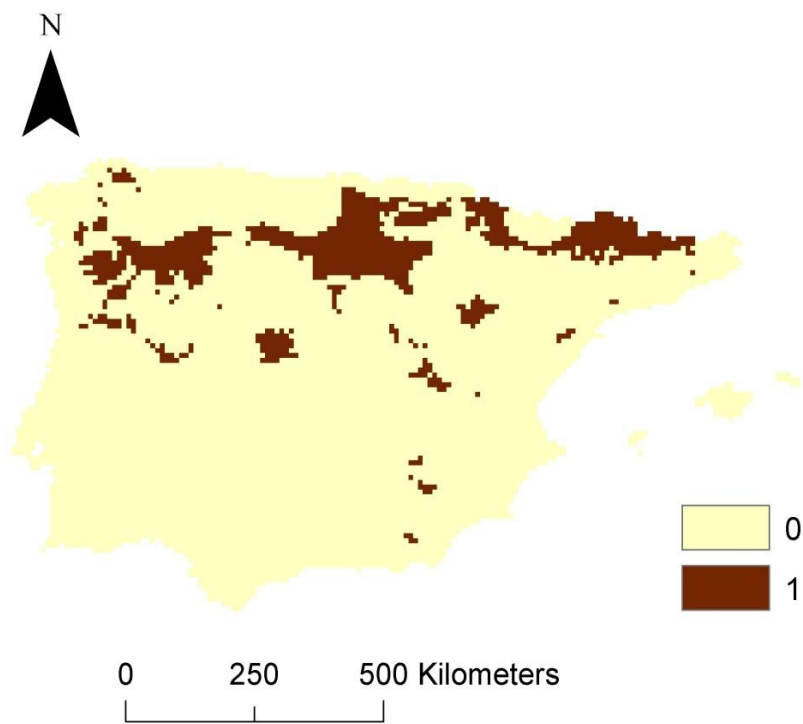
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926 Figure S2.8. *Bombus cullumanus*



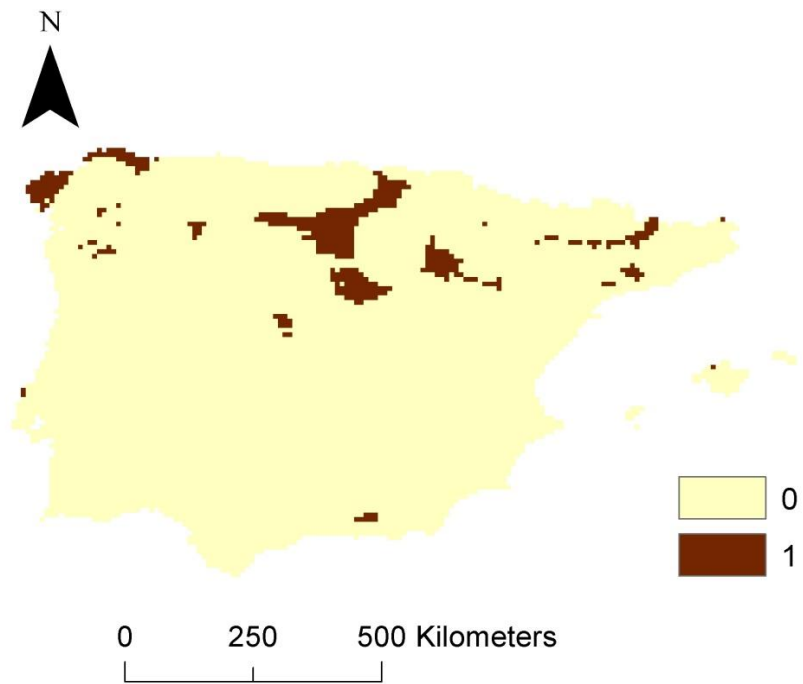
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928 Figure S2.9. *Bombus barbutellus*



929

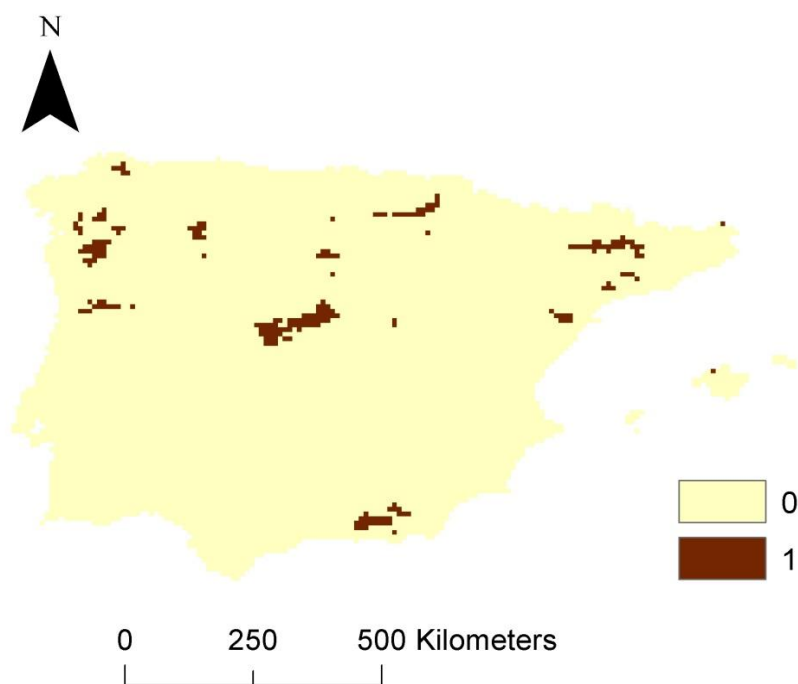
930 Figure S2.10. *Bombus humilis*



931

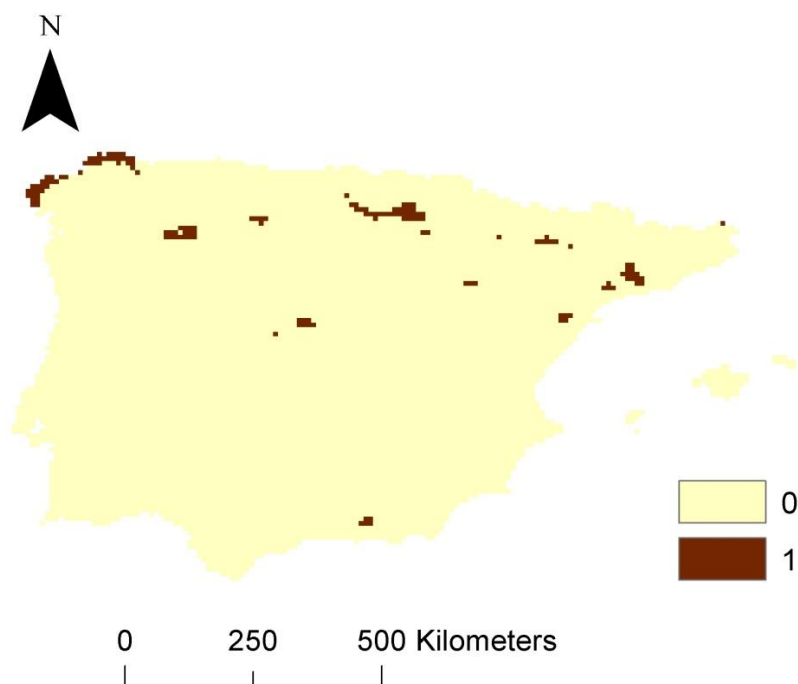
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933 Figure S2.11. *Bombus lapidarius*



934

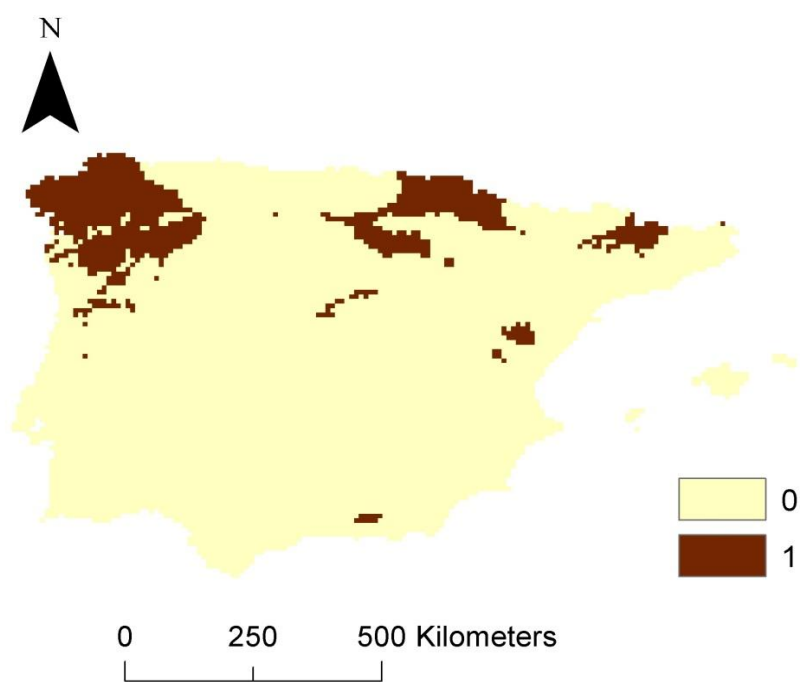
935 Figure S2.12. *Bombus sylvarum*



936

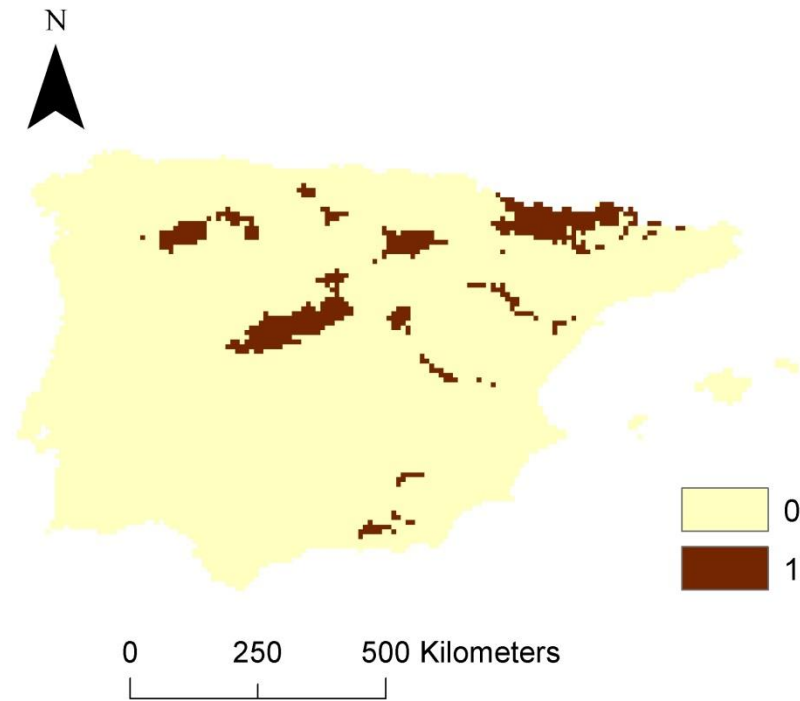
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938 Figure S2.13. *Bombus campestris*



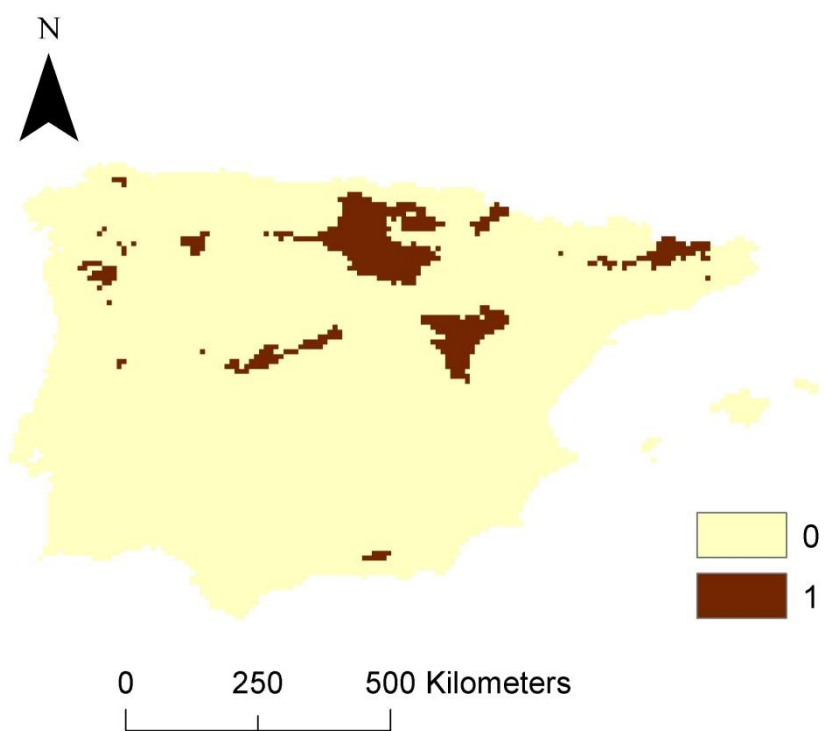
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940 Figure S2.14. *Bombus mocsaryi*

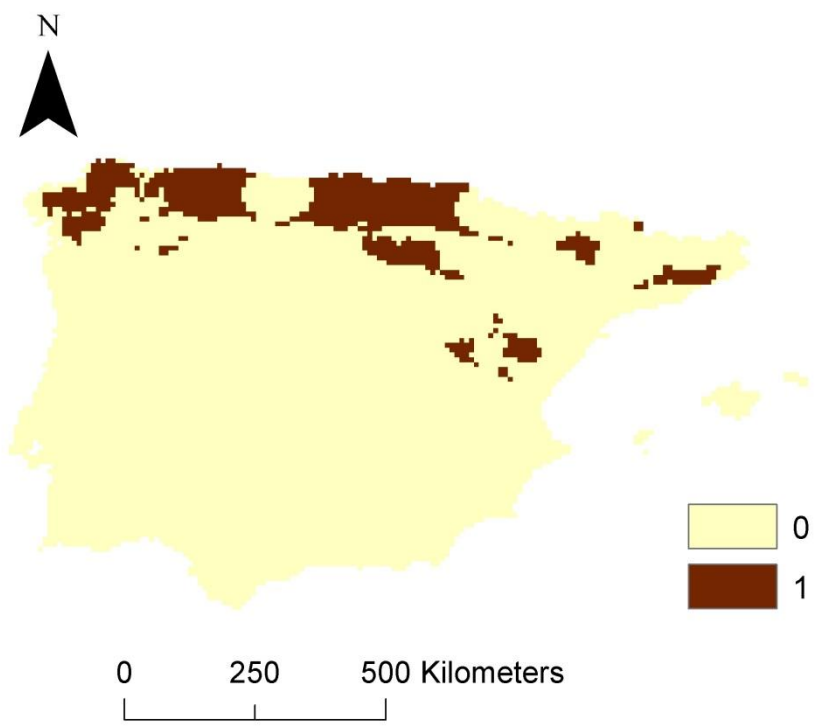


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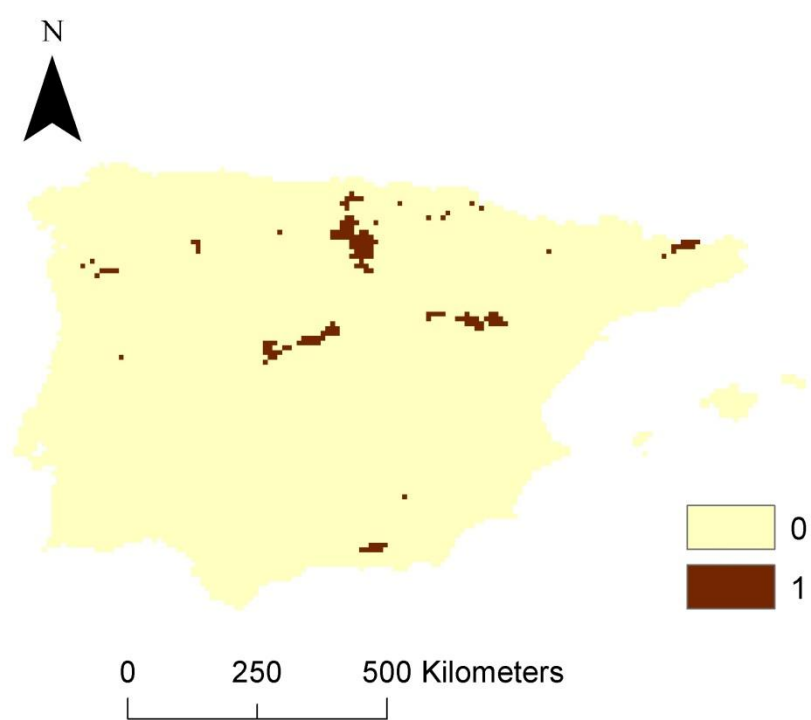
952 Figure S2.15. *Bombus sylvestris*



963
964 Figure S2.16. *Bombus confusus*

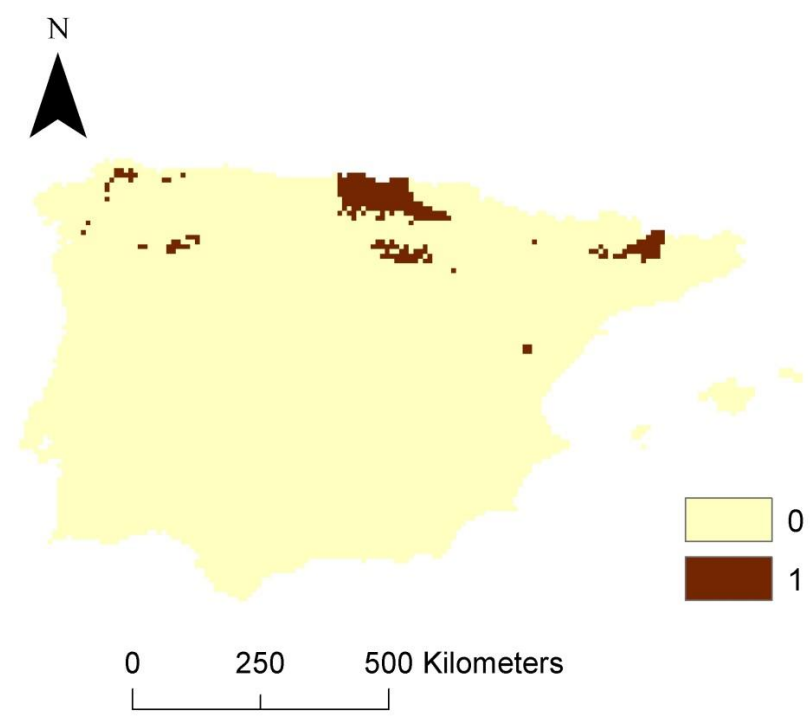


974 Figure S2.17. *Bombus rupestris*



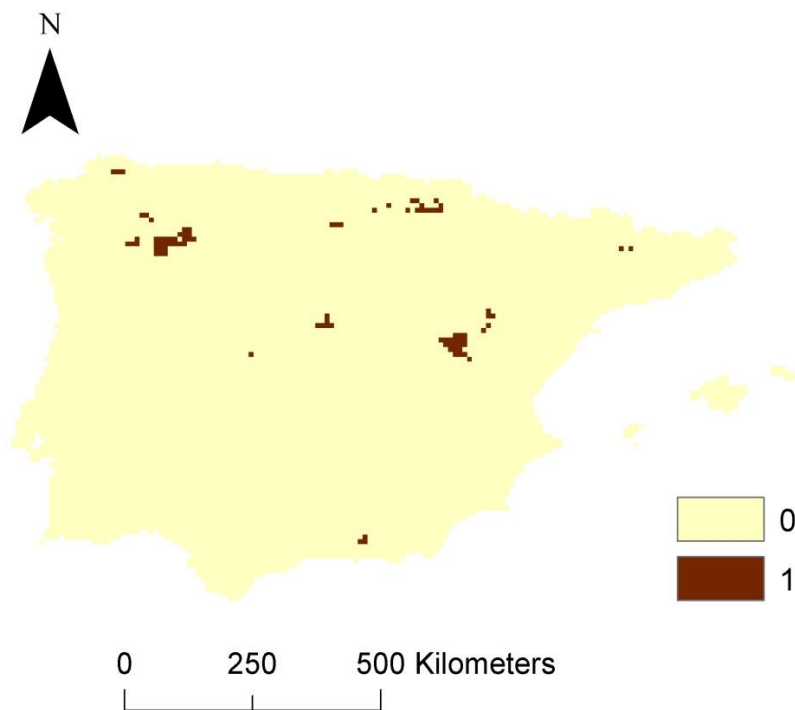
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986 Figure S2.18. *Bombus hypnorum*



987

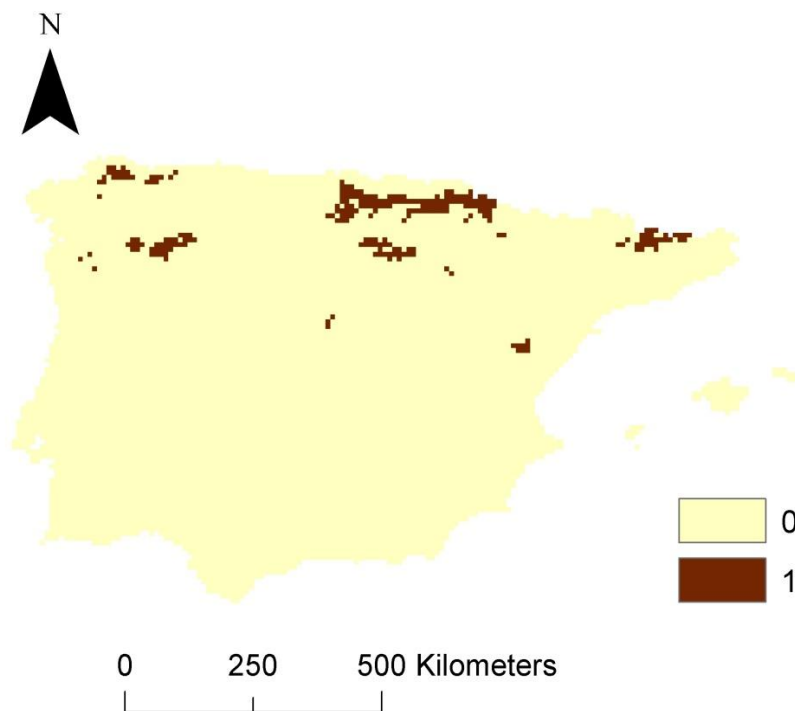
988 Figure S2.19. *Bombus ruderarius*



989

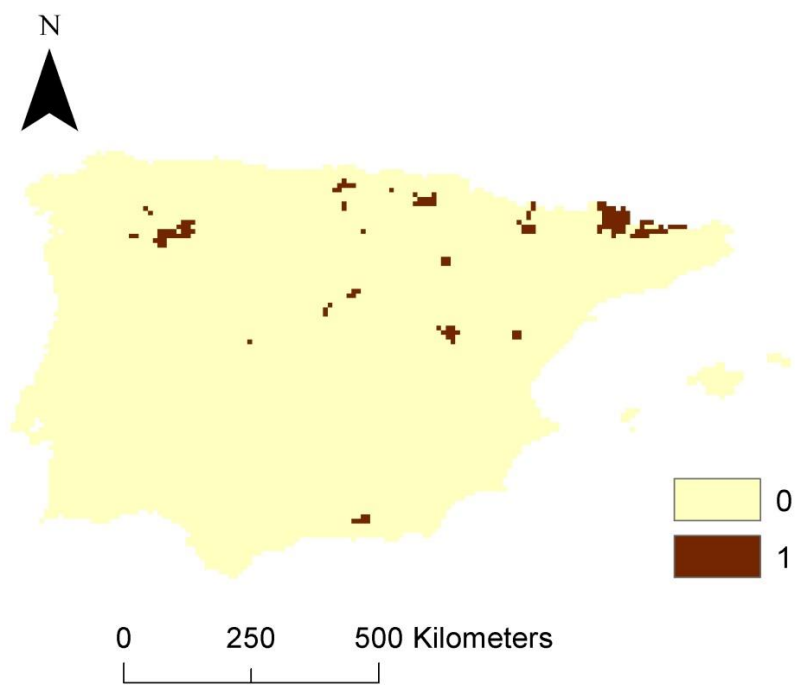
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991 Figure S2.20. *Bombus wurflenii*

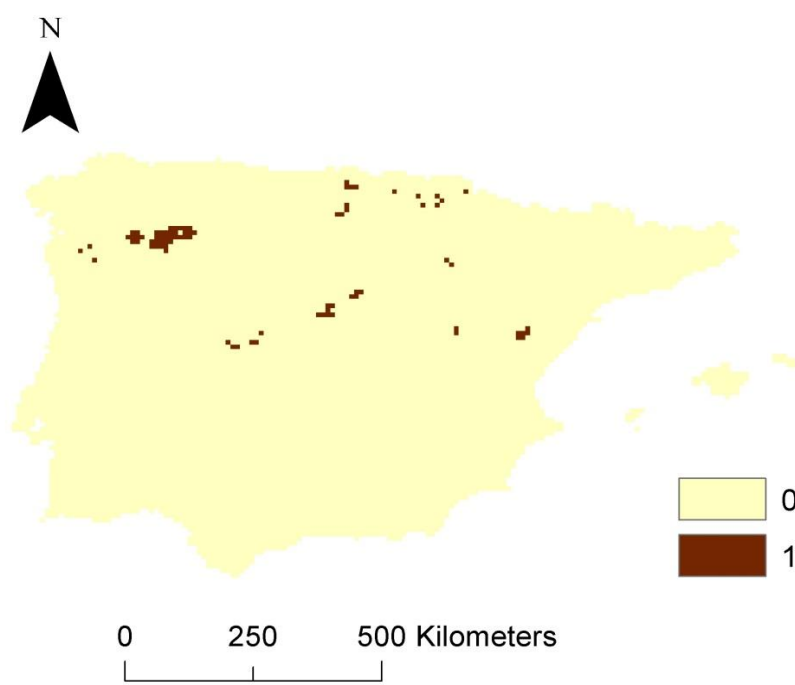


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993 Figure S2.21. *Bombus jonellus*

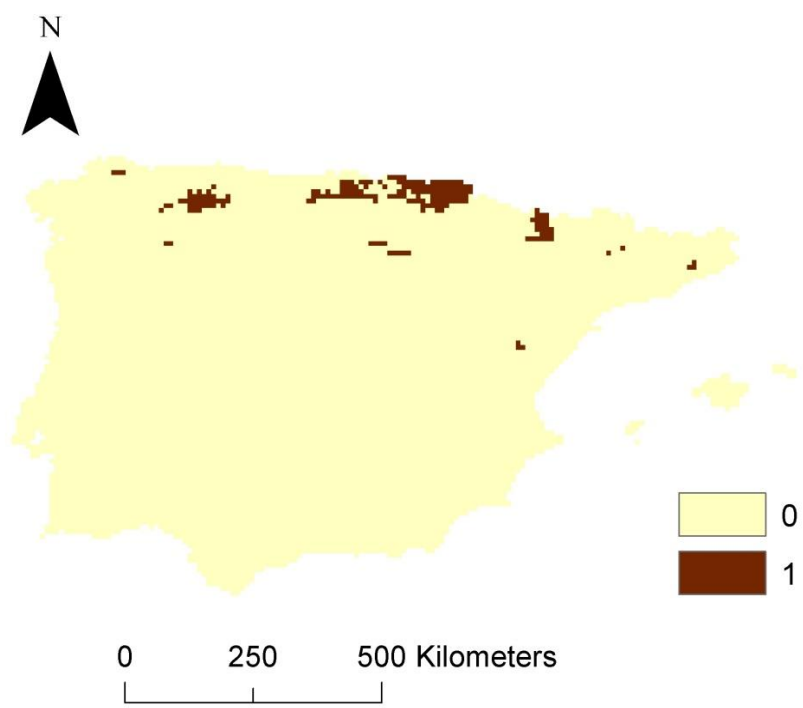


994
995 Figure S2.22. *Bombus mesomelas*



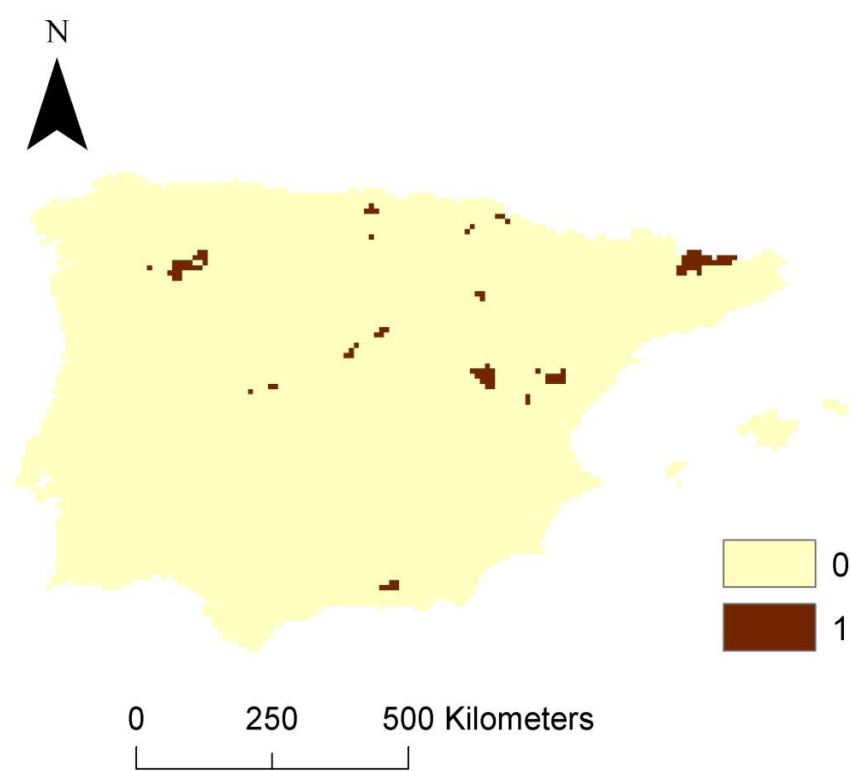
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999 Figure S2.23. *Bombus mendax*



1000

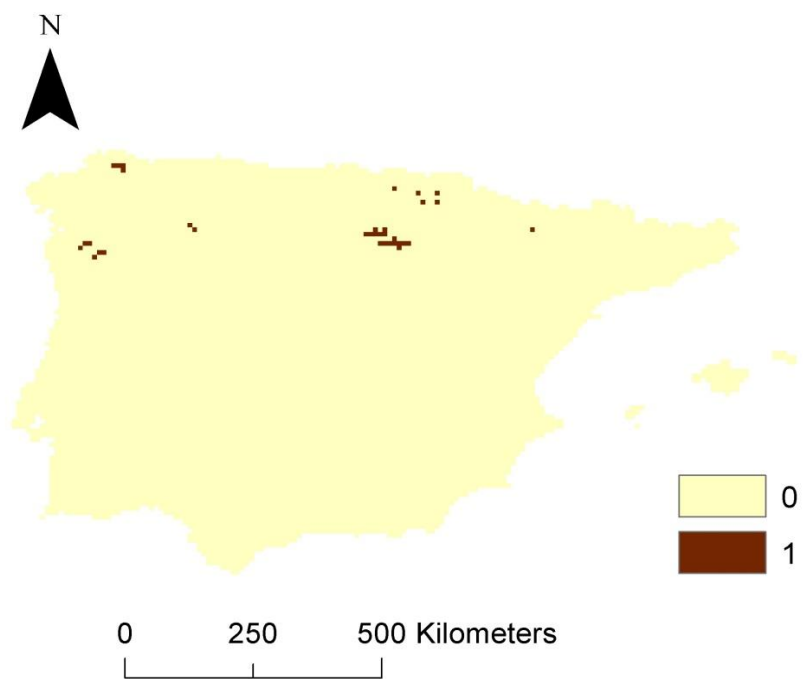
1001 Figure S2.24. *Bombus bohemicus*



1002

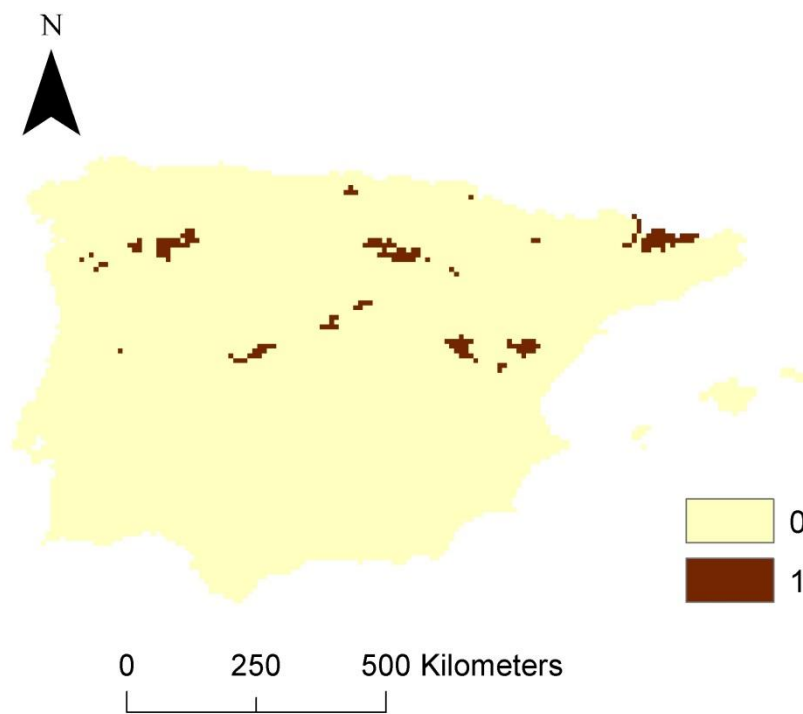
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1004 Figure S2.25. *Bombus soroeensis*



1005

1006 Figure S2.26. *Bombus quadricolor*

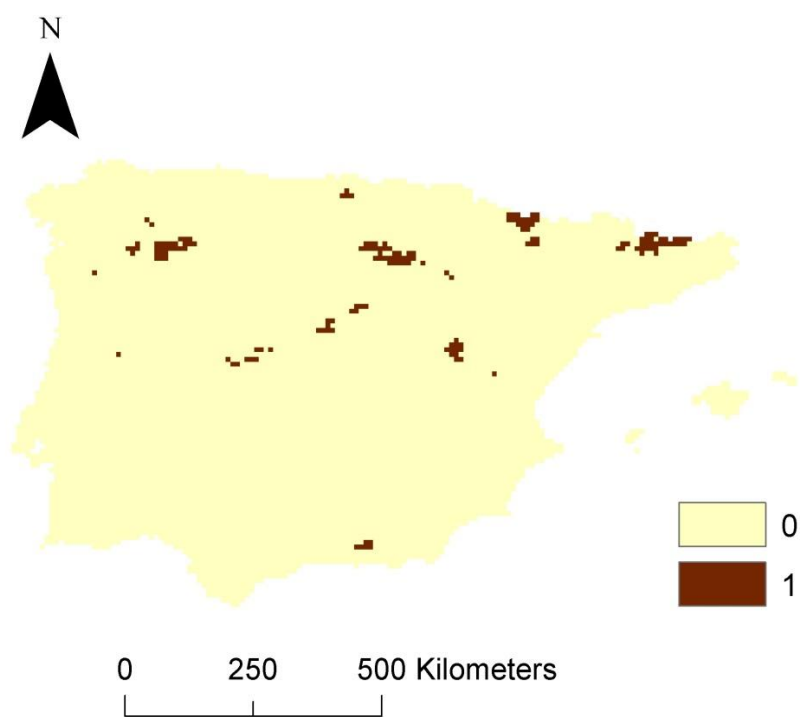


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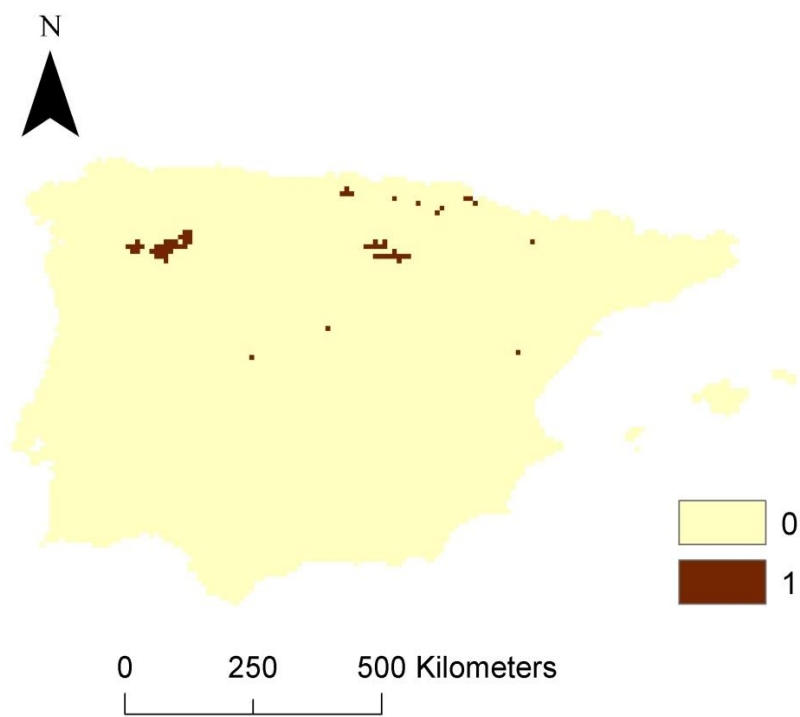
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1011 Figure S2.27. *Bombus subterraneus*



1012

1013 Figure S2.28. *Bombus sichelii*

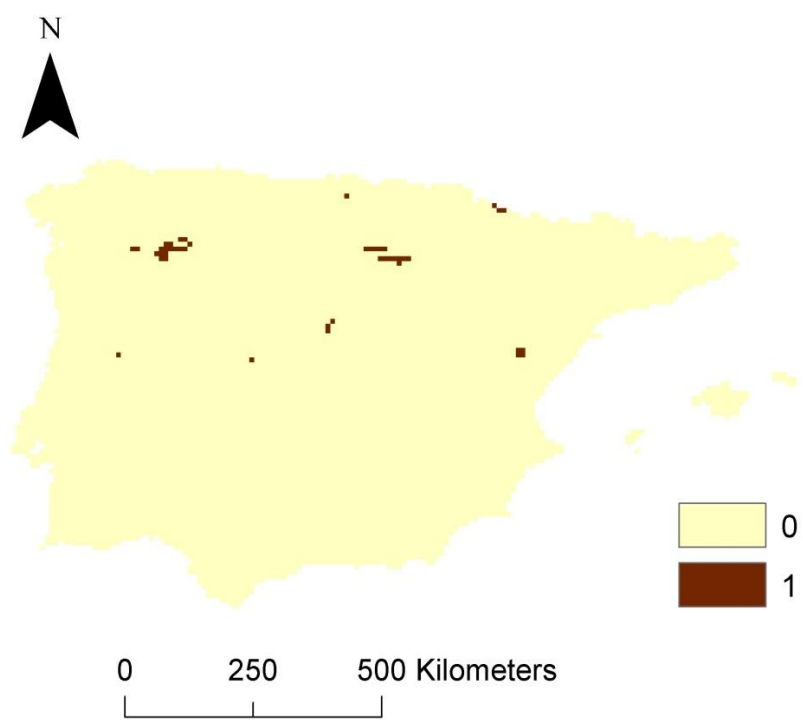


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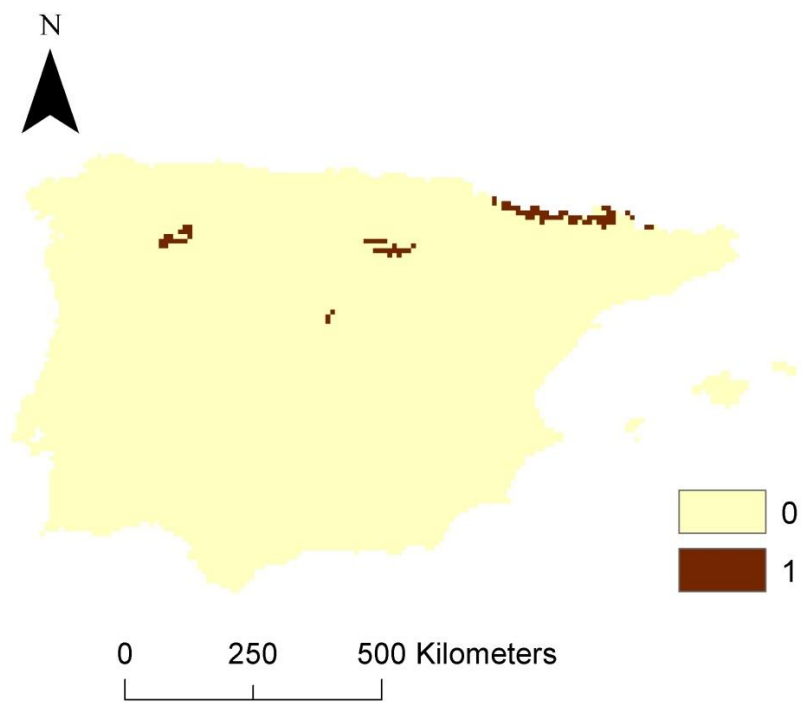
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1017 Figure S2.29. *Bombus monticola*



1018

1019 Figure S2.30. *Bombus inexpectatus*

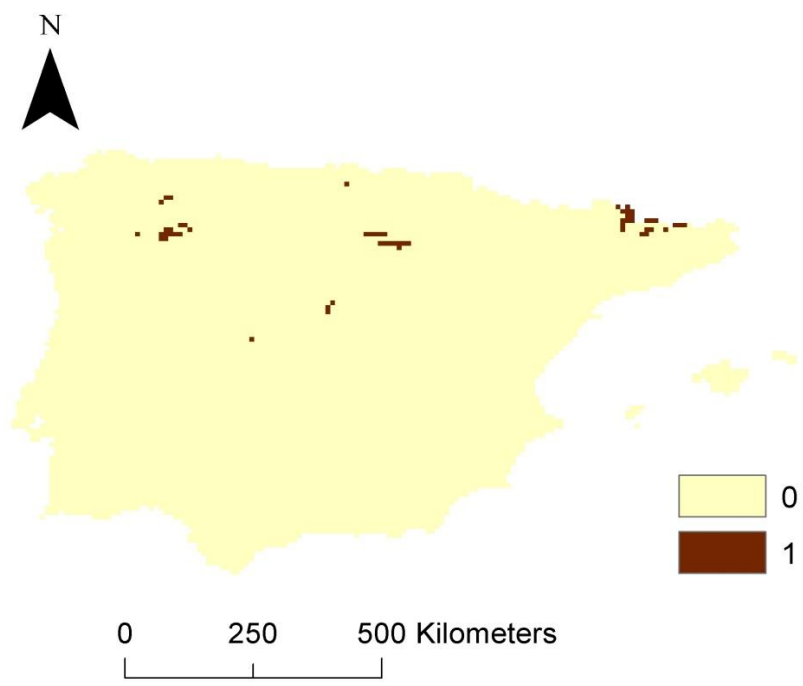


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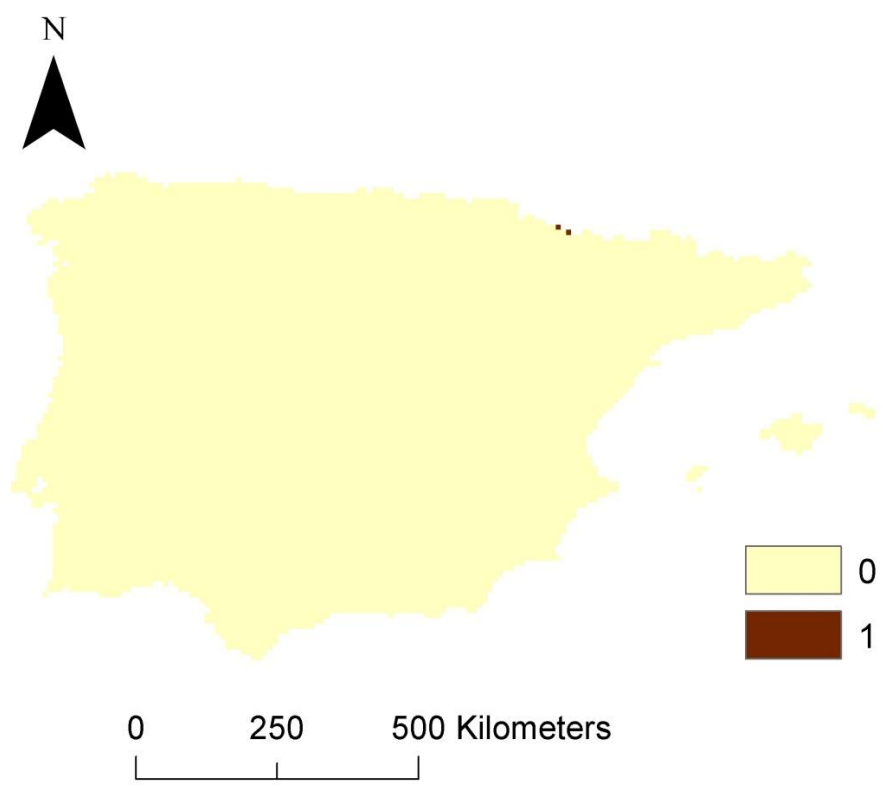
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1023 Figure S2.31. *Bombus mucus*



1024

1025 Figure S2.32. *Bombus pyrenaicus*



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1027